Pyramimonas gelidicola: Its potential as a climatic indicator.

By: Serena Fulford-Smith

MSc Student

IASOS

University of Tasmania

Declaration:

I hereby declare that the work in this thesis is my own except where referenced in the text. This work is not substantially the same as any other which has been published or submitted as thesis research at any other University.

Serena Fulford-Smith

Acknowledgments:

It is always the author's prerogative to thank the people who have made the completion of their project possible.

Firstly, I would like to thank Liz Sikes, who not only gave up hours of her time for proof reading and editing, but who also gave me confidence and pride in my work. Many thanks to Sue Blackburn for her advice and help with culture results and also to Gerry Nash, who was patient and always available to show me the intricacies of the Antarctic Division E.M Lab and dark room. Harry Burton supplied the original idea of the project and John van den Hoff was wonderfully resourceful in fulfilling its logistical demands. Andrew McMinn helped with the structure of the sediment core experiments and the cores and additional dating was supplied by Michael Bird from the School of Physical Research at ANU.

I wish to express my thanks to my family and friends, the staff and past and present students of IASOS, who have been a pleasure to be associated with and have shown both interest and support over the past two years.

Last, but by no means least, many thanks to my husband who survived these last two years by being supportive and supremely tolerant especially over the final days.

This project was funded by a CRC grant as part of the Natural Variability sub-programme.

Table of contents:

Chapter 3:

An examination of the evolution of Ace Lake from a sediment core.

Chapter 4 :

Conclusions

Bibliography

Appendix

Figures:

Plates:

Abstract:

Pyramimonas gelidicola has a wide distribution in the Vestfold Hills, and because the body and cyst scales of the species are preserved in sediments, it has been believed to have some potential as a tool for palaeoclimatic research. This potential will be tested in this study. Two strains of Pyramimonas gelidicola were examined to determine the physiological conditions that promote encystment in this species. These results were coupled with an examination of the P. gelidicola scale concentrations in an Ace Lake sediment core and the diatom stratigraphy of that core, in order to determine the evolution of the lake.

P. gelidicola is a robust species, it thrives in a broad range of physiochemical conditions. It is a euryhaline species which grows in a range of salinities from 5 to 80‰ with an optimal salinity range of 35-60‰. P. gelidicola survives in temperatures from -1.5 to 18°C and is at an optimum at 6-8°C. This species grows in nutrient conditions of F_{50}-2F with optimal growth at F and F_2 and appears to be shade adapted to 10 $\mu Em^{-2}s^{-1}$. Cysts occurred in all treatments regardless of growth phase, most were produced in optimal nutrient and hypersaline conditions. Because of the wide growth tolerances of this species and the conflicting cyst production, its use as a palaeoclimatic tool may be limited.

Analysis of Pyramimonas gelidicola scales and diatom frustules in the sediment indicates that Ace Lake was first isolated 8100-9200 years ago, underwent a freshwater and a restricted marine phase, and finally became a stable meromictic lake 3000-4000 years ago. The vegetative cell scales and the cyst scales of P. gelidicola occur throughout the core with dominant cyst production occurring in the fresh and marine phases of the

lake. Peak vegetative cell scales occur in the last 3000-4000 years, but no cyst scales were noted in this time. A comparison of diatom stratigraphy and scale concentration results with a sea surface temperature record of the Southern Ocean (Pichon *et al.*, 1992), indicate regional changes that have occurred in the last 10 000 years show no correlation with the diatom or scale trends seen in the core. These results suggest that the lake systems of the Vestfold Hills that have been subject to marine incursions are dominated by local effects. Because these effects are so dramatic they are masking any climate changes that may have occurred in the region. Therefore, studies of regional climate are more appropriate in the open ocean where conditions are more sensitive to climate changes.

Chapter 1:

Background:

1.1 Introduction:

The Antarctic continent plays a major role in the climate of the Southern Hemisphere (Pook, 1989, Pichon *et al.*, 1992). Covering a total area of 20 million kilometres square in winter, the continent and its surrounding ice cover act as a heat sink. This phenomenon is more pronounced than in the northern hemisphere because the continent is pole centered and has a high mean altitude of 2500 metres. The impact this has on the circulation systems of the southern hemisphere is two fold: circulation patterns introduce a net heat input into higher latitudes and create a strong temperature gradient, especially during equinox periods (Pook, 1989): additionally the brine drainage from the seasonal ice formation around the continent causes the thermocline convection and deep vertical mixing in the oceans (Allison, 1989). Because of the isolation of the continent and it's historical connection with other continents through the Gondwana complex (Quilty, 1985), the Antarctic continent has preserved a data base of global climate change (Ice core data). Therefore, an investigation into the climate of the continent during the Holocene is invaluable as a tool for gauging both the climate change of other continents in the past and as a tool for predicting climate change in the future.

The lakes of the ice free oases in Antarctica provide in their sediments a continuous record of the changes that have occurred in the lakes since they became ice free 8000 years ago (Pickard *et al.*, 1986). As the Antarctic lakes are subject to little bioturbation and reworking, their sediments record the phytoplankton assemblages of the lakes at the time of deposition and so can give insight into the evolution of the lakes since the ice retreat.

Diatoms are often used in palaeoclimatic research on sediment cores as they have siliceous exoskeletons which are easily preservable and recognisable. They inhabit very selected niches in the open ocean water column (Leventer and Dunbar, 1988, Fryxell, 1989, Stockwell *et al.*, 1991) and by utilising the information on their present day habitat, the diatom composition of the sediments can be used to indicate past conditions and changes such as ice cover or variations in water level that have occurred in the past (Leventer and Dunbar, 1988). In lakes however, diatom species are limited to neritic epontic marine genera, such as Nitzschia or freshwater species, such as Stauroneis and P. microstauron. Therefore, the diatom changes in a lake core can only be used to infer physical changes such as salinity, or broad scale variances such as marine incursions and ice cap movements brought on by global warming or cooling.

This study focuses on the Pyramimonas gelidicola strain found in Ace Lake and the scales of that species in an Ace Lake sediment core. Pyramimonas gelidicola is the most comman prasinophyte species found the Southern Ocean (Mc Fadden *et al.*, 1986). It has a wide distribution from the sea ice fringes to the lakes and fjords that dot the continent. Little is known of the physiology of the species; it is not abundant in the Antarctic marine ecosystem, but is often the dominant plankter in the continental lakes.

This study examines Pyramimonas gelidicola to determine if the cyst scales of this species indicate a particular lake environment and therefore can be used as a climate indicator in Antarctic lakes, particularly the lakes of the Vestfold Hills. This species was chosen because of it's broad distribution in the lakes across the Vestfold Hills (van den Hoff *et al.*, 1989) and it's presence in Antarctic marine environments (McFadden *et al.*, 1982).

1.1 Vestfold Hills (69°33'S-78°15'E):

The Vestfold Hills were first discovered and named in 1935 by Klarius Mikkelsen, the captain of the Norwegian Ship, Thorshavn. However, very little research was carried out in the Vestfolds until 1954, when the Australian National Antarctic Research Expeditions (ANARE) landed their first expedition in the region and three years later built Davis station.

The Vestfold Hills cover a total area of approximately 410 km^2, bordered to the south by the Sorsdal glacier, to the east by the ice cap and the west by Prydz Bay (Fig 1.1) The maximum altitude of the Vestfold Hills is 157m at Boulder Hill. Despite this elevation, the exposure of land in the Vestfolds is continuously low and undulating with most of the area incorporated in the three peninsulas, Long, Broad, and Mule. The Vestfold Hills are free of permanent ice and snow the year round because of ablation. It is this phenomena and the lakes that dot the majority of the exposed area that led to the original description of the Vestfold Hills as an "oasis" (Heywood, 1977).

The Vestfold Hills are part of the 5% of the Antarctic continent that is ice free. Hence, they are of importance, as a "window" into Antarctica's geological history. The East Antarctic region is made up of a Precambian continental shield (James and Tingey, 1983), with an overlay of younger sedimentary and volcanic rocks, which have been criss-crossed by metamorphic mafic dykes (Adamson and Pickard, 1986a). The sediments of the Vestfold Hills have been studied extensively because of their importance in the dating of glacial action and the reconstruction of palaeoclimates. The glacial sediment and striae of the Vestfolds are indicative of the time and direction of the last Pleistocene glacial action. Adamson and Pickard (1986b) determined from these striae that the main ice advance in the area was WNW, at right angles to the contours of the ice sheet.

The Vestfold Hills are the main source of tertiary marine sediments on the East Antarctic Shield. Up to 30% of the total area of the Hills is covered by Pleistocene and Holocene glacial sediments (Adamson and Pickard,

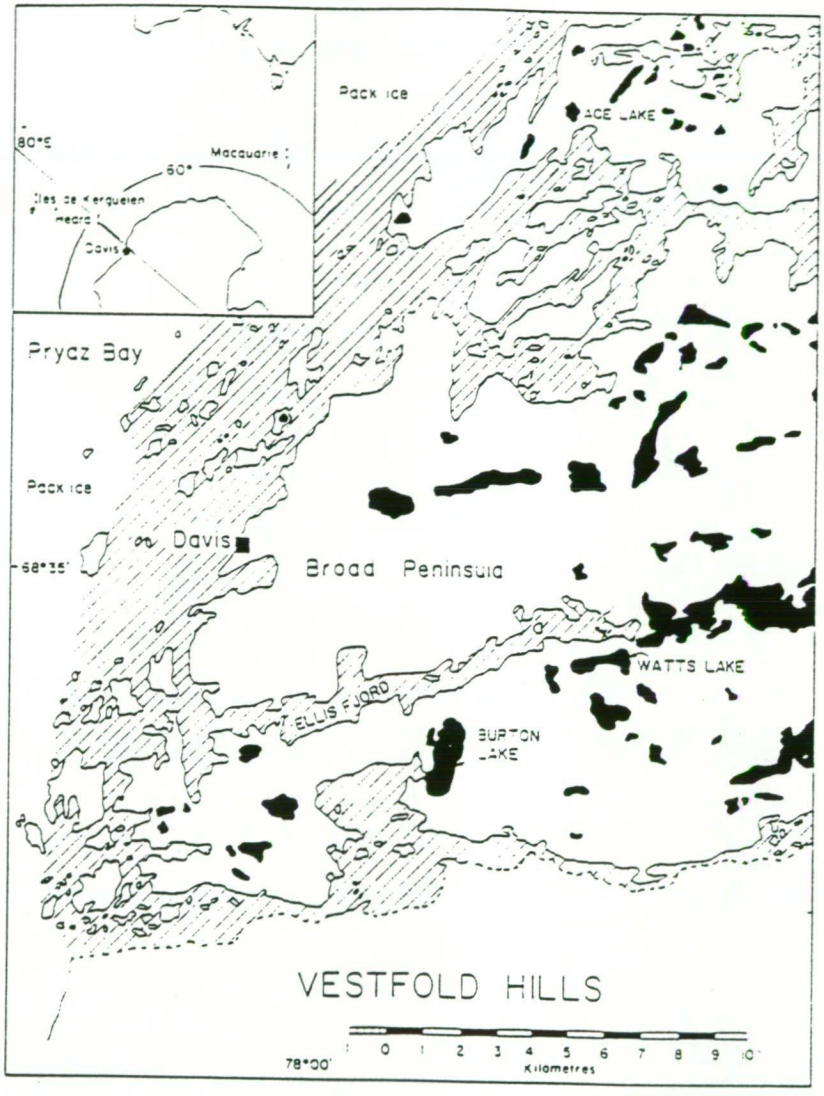


Fig 1.1: Map of the Vestfold Hills

(after Burton and Barker, 1978)

1986b). During the Pleistocene it is hypothesised that the Vestfold Hills were covered by an ice sheet up to 1000m thick that extended to the edge of the continental shelf and incorporated a number of the offshore islands (Adamson and Pickard, 1983). The global warming that occurred at the end of the Pleistocene would have caused the ice sheet to melt and retreat. Due to the altitude of the Vestfold Hills the ice streamswould have had to divert around them, so that as the overlying ice sheet thinned it left the area bare (Solopav, 1969). As the ice sheet retreated, in conjunction with the northern hemisphere ice cap retreat, the land flooded as the sea level rose. After the weight of the ice sheet was removed, isostatic uplift occurred, exposing the coastal regions and trapping sea water in the valleys, forming the lakes and fjords of the Vestfold Hills.

The Vestfold Hills have a maritime climate and are therefore less extreme than the inland oases, such as Wright Valley (Streten, 1986). Coastal stations can be up to 4°C warmer than inland stations with an average difference of 1-2°C on a monthly average (Streten, 1986). There are two main factors that affect the climate of the Vestfold Hills, the ice cap to the east and the cyclonic depression that occurs in Prydz Bay. The presence of the depression in the bay is influenced by the topography of the region and in particular by the proximity of the Lambert glacier (J. Nairn, *pers. comm.*). This low pressure system occurs seasonally, fluctuating off the coast in sequence with the movement of the Antarctic trough. During summer and autumn when the Antarctic trough is closest to the coast, the moist onshore winds of the depression in Prydz Bay mix with the katabatic winds of the continent to form a warm front. This warm front is characterised by north easterly winds which cause an increase in ablation at the coast and an increase in precipitation as the warm front moves inland (M. Pook, *pers comm.*).

The katabatic winds generated from the continental ice sheet are less extreme across the Vestfold Hills than at other coastal regions such as Mawson base, due to the large exposed area of ground between the ice sheet and the shore. This means that drift and ablation are lessened as the winds are warmed by the ice free ground as they move to the coast (Streten, 1986). These winds reach speeds of 51 km/hr as the cyclonic

depression moves away from the coast following the seasonal movement of the Antarctic trough in spring and winter (Streten, 1986). The ablation and drift caused by the katabatic winds decrease the accuracy of any precipitation measurements on the Antarctic continent. This is especially so in the ice free areas where evaporation is higher. Because of the low precipitation, mild temperatures and high evaporation, absolute humidity in the Vestfold Hills is low (Burton and Campbell, 1980). The high evaporation and low precipitation of the ice free areas cause a decrease in lake levels and a concentration of their salt content leading to the formation of the hypersaline lakes which dot the Vestfold Hills terrain. The temperature of the region is mild for Antarctica, with an annual mean of ⁻10°C and monthly means of 0.5°C - ⁻18°C (Streten, 1986). However, the dark bare rocks of the region act as a heat sink and can reach temperatures of 20°C, back radiating heat and causing the ambient temperature to rise by up to 5°C (Streten, 1986). Even though the rocks act as a local heat source, many lakes in the Vestfold Hills maintain an ice cover all year round. The climate and wind direction of the Vestfold Hills are thought to have been fairly constant over the past 6000 years probably due to the regular presence of the depression in Prydz Bay (Streten, 1986; Pickard *et al.*, 1968).

1.2 Lakes of the Vestfold Hills:

Many of the lakes in the Vestfold Hills have a sediment history that extends back 6000-8000 years, when the area was first exposed and the present phase of rebound began (Pickard, *et al.*, 1986). Studies of these sediments have shown that broad changes have occurred since these lakes were formed. The region is dotted with hundreds of lakes, ranging in salinities from fresh to hypersaline. The largest, Crooked lake, is up to 10 km in length and over 140m deep (Hand and Burton, 1981). The majority of these lakes are freshwater, a result of localised seasonal melt water. Most fresh water lakes are believed to have been formed initially by the trapping of marine water through isostatic uplift. They then became fresher through the progressive flushing of the lake with melt water. Other freshwater lakes evolved through flooding of glacial depressions by melt water. Eight percent of the Vestfold Hills area is covered by freshwater lakes, accounting for 80% of the total number of lakes in the

area (Pickard *et al.*, 1986). Freshwater lakes often freeze over almost entirely throughout winter and are inundated with melt water throughout summer. Some of these lakes have a short turnover time and tend not to accumulate nutrients, and therefore do not develop a wide plankton or benthic assemblage. Others which are more stable develop cyanobacterial mats and sustain freshwater plankton assemblages (Watts Lake; Heath, 1988).

Saline lakes of the Vestfold Hills range from low (14‰) to high salinity (130‰) (Burton, 1981). Hypersaline lakes are believed to have been formed when the pockets of marine water isolated by isostatic uplift received little melt water input and were subject to high rates of evaporation because of the dry climate of the Vestfold Hills. Evaporation lowers the lake levels and consequently increases the salinity (eg. Deep lake). The saline lakes that have a melt water input develop fresher surface waters (eg. Ace Lake), which tend to freeze during the colder months of the year. This ice cover prevents the mixing of the lake and therefore, when ice covered, the lakes are stratified. This stratification is often permanent as the majority of the lakes are closed systems, ie. they do not have any input or run off. Because of this they become permanently stratified (meromictic). The mixolimnia and monimolimnia within the lake are separated by a transition zone called the epilimnia (Fig 1.2). These layers within the lake are formed by various physiochemical mechanisms and can be described on the basis of oxygen, temperature or salinity differences, and they can be seasonal or permanent occurrences within the lake (Burton, 1981). Meromixis in a lake is maintained by either a large halocline, pycnocline or oxycline in summer and usually ice cover in winter (Burton, 1981). Hypersaline lakes are often stratified during the summer months because of the formation of a pycnocline, but, as they don't form an ice cover in winter, they become holomictic (Gallagher, *et al.*, 1989).

The process of isolation of a lake from the marine environment can be seen today. Fjords like Ellis have shallow connections with the sea, and are therefore restricted and meromictic in parts. The basins within the fjords and other marine coastal areas, when isolated by isostatic uplift, become

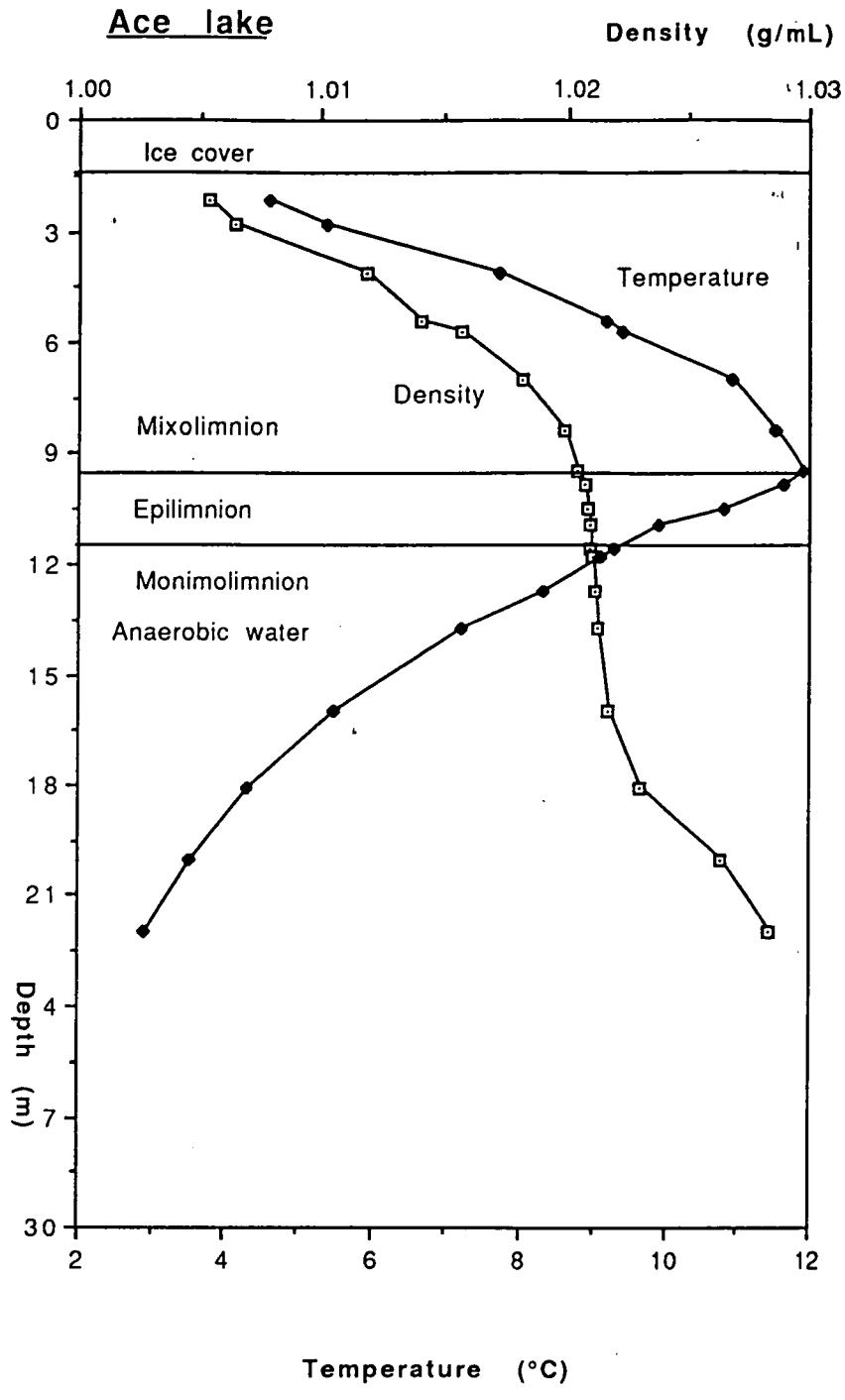


Fig 1.2: Ace Lake Density Profile

(after Fulford 1990)

tidal lakes, such as Burton, Fletcher, and Rookery Lakes, which all have a seasonal connection to a marine source. This means that they become meromictic and periodically receive a marine water influx to replenish both the species assemblage and the nutrients in the lake (Eslake *et al.*, 1991). Any change in the land elevation or sea level and they then become a closed system limiting the biota able to live in them (Bird *et al* ., 1991).

The development of the lake after isolation depends on the melt water input and the ionic input the lake receives. Both saline and freshwater lakes receive nutrients from erosion of the rock basins by meltwater or the chemical leaching and weathering of the marine sedimentary basin (Heywood, 1977). The sea is an important source of wind blown ions to coastal lakes, especially as precipitation in Antarctica is so low (Masuda *et al.*, 1988). The isolated lakes therefore have a high relict salt content (Burton, 1981) and because they are coastal, their salinity is replenished mainly by sea spray with smaller inputs from the weathering of the lake basin. If they are not part of a drainage system, such as Druzby, they would have a low seasonal freshwater input, high evaporation and low precipitation and seasonal brine production, which would cause the salinity to increase forming hypersaline lakes. Lakes that were not subject to a marine incursion may also become saline if the drainage pattern they were associated with changed course (M. Bird *pers comm.*), because of the same processes mentioned above.

The phytoplankton assemblages of the freshwater and saline lakes of the Vestfold Hills are often simple, sometimes without grazers therefore, production is often limited only by the physical parameters of the lakes and the Antarctic climate. The stratified saline lakes are often oligotrophic and contain only a few species of eukaryotic organisms (Wright and Burton, 1981). Diatoms are the dominant organisms; the most common genera are Navicula, Nitzschia, and Chaetoceros (Fulford, 1990). The prasinophyte Pyramimonas gelidicola has been recorded in at least 20 lakes in the Vestfold Hills (van den Hoff *et al.*, 1989). The low species diversity in the saline lakes of the Vestfold Hills is not representative of all lakes in the region. Diatoms are better represented in the freshwater lakes of the sub antarctic islands and the Antarctic continent (Oppenheim and

Pugh, 1987, Wasell and Hakansson, 1992). The dominant plankters, Chlorella and Chlamydomonas, as well as 10-20 species of diatom, have been found to dominate the benthic mats of freshwater lakes and the fresh mixolimnion of meromictic lakes (Parker *et al* ., 1977, Oppenheim and Pugh, 1987). There is a large diversity of diatom species as well as dinoflagellates, prasinophytes, coccolithophorids and pymnesiophytes in the inlets and fjords around the Vestfold Hills (Everitt and Thomas, 1986, McMinn *et al.*, in prep). This would suggest that the evolution of the lakes since their isolation from the sea has reduced their diatom composition. Lee (1980), suggests that the changes in the nutrient concentrations, such as silicas and vitamin B^{12} and the increase in salinity since the isolation of the lakes have made them unsuitable habitats for the majority of the marine diatom species.

1.3 Ace Lake:

Ace Lake is a saline meromictic lake, situated on Long peninsula in the Vestfold Hills (Fig 1.1). The lake covers an area of 0.132 km^2 in a catchment area of 0.511 km^2. It has a maximum depth of 22.5 m and an oxylimnion at 11 m. The salinity of the lake ranges from top to the oxycline: 9 - 29.8 ‰, and the temperature from 4.9 - 9.9 °C (Burch, 1988). Volkman *et al.*, (1988), quotes a water level increase of 1.5 metres over the period of 1977-1988. This increase could be due to the localised melt water received by the lake from snow that blows off the plateau and is trapped in the lee of the surrounding mountains, forming snow banks which melt in spring (J. Gibson, *pers. comm.*). Therefore, a local increase in precipitation or an increase in ablation would lead to increased melt input. Unfortunately, this is only speculation as precipitation and ablation are difficult to accurately measure in Antarctica and no attempt has been made to measure precipitation on Long peninsula (S. Pendlebury, *pers comm.*).

Ace Lake has four features that make it useful for palaeoclimatic study: first, it is isolated from any anthropogenic input; second, it is a closed system with an anoxic basin preventing any reworking or bioturbation of the sediments; third, the phytoplankton community of the lake is well documented and fourth, the lake is stratified indicating no reworking of the sediments. The area surrounding the lake has little vegetation and

therefore there is no contamination of the lake derived flora in the sediments from in-blown material. Because the lake is a reasonable distance from the nearest base of human activity the impact in the area has been minimised. There have been numerous previous studies on the plankton assemblage in the lake, which can be used in the interpretation and analysis of this project and also, other studies on the lakes of Antarctica have completed examinations of the sediment of the lake (Bird *et al.*, 1991) .

Burton and Barker (1978), examined the plankton assemblage of Ace Lake in conjunction with a study of sulphur isotopes finding a dominance of diatoms, mostly Fragilaria sp. and Navicula sp in the assemblage. Further study by Volkman *et al* ., (1988) found that the phytoplankton assemblage of Ace Lake was comprised of only four species; a pymnesiophyte, a dinoflagellate, Cryptomonas sp. and Pyramimonas gelidicola. They found no presence of diatom derived compounds in their HPLC studies but did report a few cells in preserved lake samples. Burton and Barker (1978) also noted the presence of two zooplankter; Paralabidocera antarctica and Acartia sp.

The report of the presence of Acartia sp. in the lake was not confirmed by Bayly and Burton (1987), who only found P.antarctica. Mancuso *et al* ., (1990), found evidence of a variety of diatom species not noted in the plankton assemblage of Ace Lake in their lipid analysis of the surface sediments of the lake. The conflicting reports on the presence of diatoms in the lake could be due to their association with the benthic mats that cluster the edge of the lake, this would limit their distribution in the water column over time, thus affecting sampling results (J. Gibson, *pers. comm.*).

1.4 The Prasinophyte: Pyramimonas gelidicola:

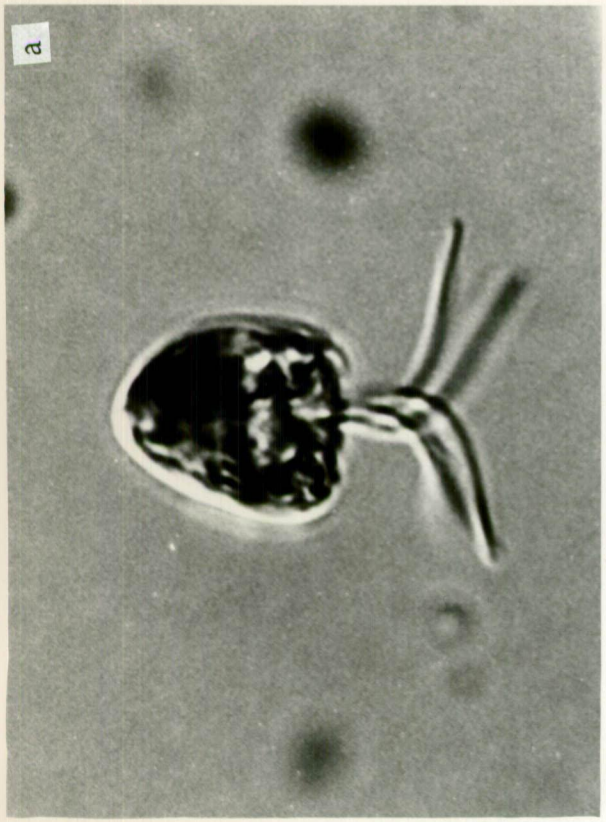
Pyramimonas gelidicola is the most comman prasinophyte found in Antarctica. It was first described by Geoffrey McFadden in 1982 from a Prydz Bay sea ice sample. It has subsequently been found in saline lakes and fjords scattered across the Antarctic continent. P. gelidicola appears conical under a light microscope, it is 14-18 μm in length and 8-9 μm in width. The cells are anteriorly rounded and four flagella arise from the

anterior depression (Plate 1.1). The main taxonomic feature used in the differentiation of Pyramimonas species are the scale types. A vegetative Pyramimonas cell can have up to seven different scale types (McFadden *et al*, 1986). P. gelidicola has three different body scales and two flagella scales. The scales are synthesised in the golgi apparatus and are released via the flagella depression (van den Hoff *et al.*, 1989). P. gelidicola vegetative cells have a lower box scale layer, an upper crown scale layer and interlinking footprint scales (Plate 1.2). The flagella have 5 hairs per μm and two different scale types; lower pentagonal scales and outer limulus-shaped scales (McFadden *et al.*, 1986).

Cyst formation in Pyramimonas species has been observed since 1938 (Korschikov, 1938). P. gelidicola is the only species that has a cyst with different scale types to the vegetative cell (van den Hoff *et al.*, 1989). This sixth type of scale is similar to the box scale but has projections from each of it's four corners (Plate 1.3). The scales are 230 x 80 nm in size and easily distinguishable under transmission electron microscopy at 20 000x. The cyst scale tends to stain positively and the vegetative scale negatively when treated with 3% Uranyl acetate. The scales of P. gelidicola, which are organic in composition, have been found preserved in sediment cores taken from Ace Lake and Prydz Bay (van den Hoff *et al.*, 1989). The ability to differentiate between cyst and vegetative scales in these sediment cores is an advantage in determining the dominant life stage of P. gelidicola in the water column at the time of sedimentation. The factors controlling the formation of cysts in Pyramimonas gelidicola and other Pyramimonas species are unknown.

The purpose of this study was to determine the cause of encystment in Pyramimonas gelidicola cultures during growth experiments and to use this information to determine if the concentration of these body and cyst scales in the sediments of Ace Lake are indicative of a specific climate change. As P. gelidicola is found across a diverse range of environments in Antarctica, the ability to use it as an indicator of change can be important in gaining an insight into the evolution of the lakes of the Vestfold Hills, which cannot be determined using their limited diatom assemblages. This study attempts to develop a technique comparable to that of diatom

assemblages and to apply it to determine the evolution of the Vestfold Hills in relation to climatic and geological changes that have occurred since the isolation of the lakes, fjords and marine environments 8100-9200 years ago.



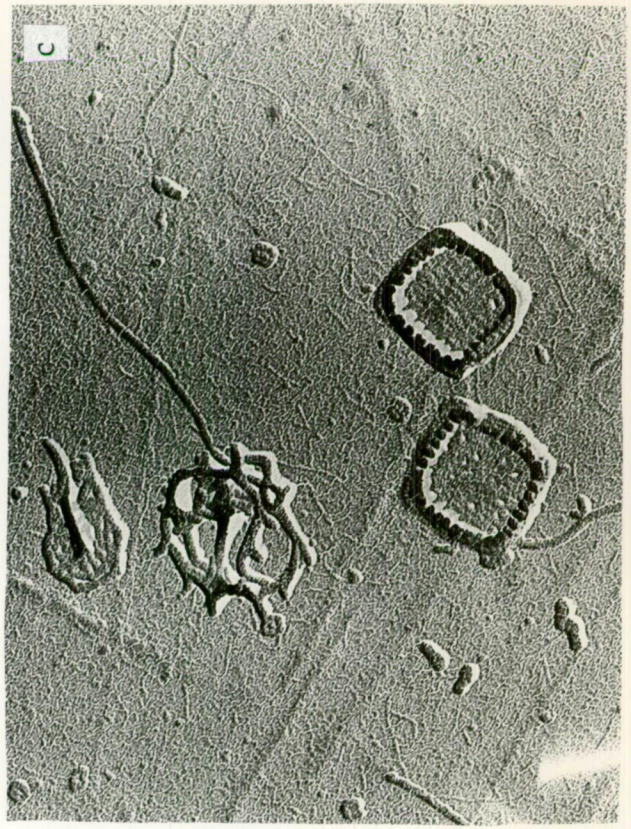
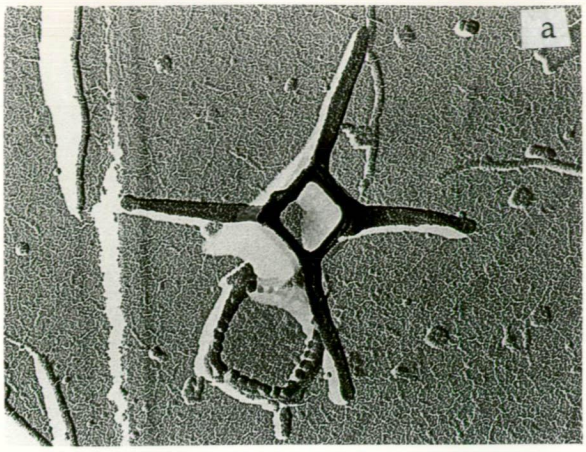
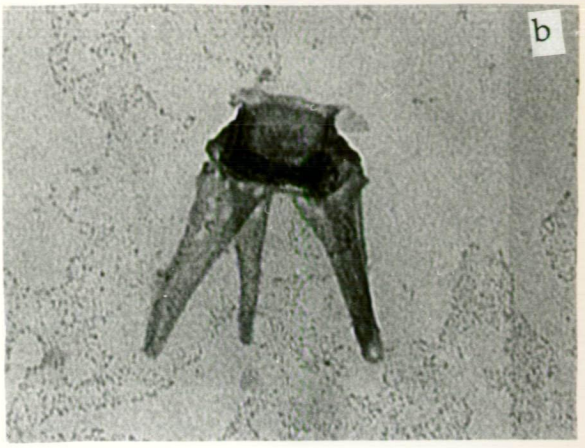


Plate 1.1a: P. gelidicola cell (8 x 14 µm). b: Anterior view of P. gelidicola cell. c: limulus shaped flagella scale (320 x 200 nm), cell crown scale (500 x 320nm), and two cell box scale (320 nm).





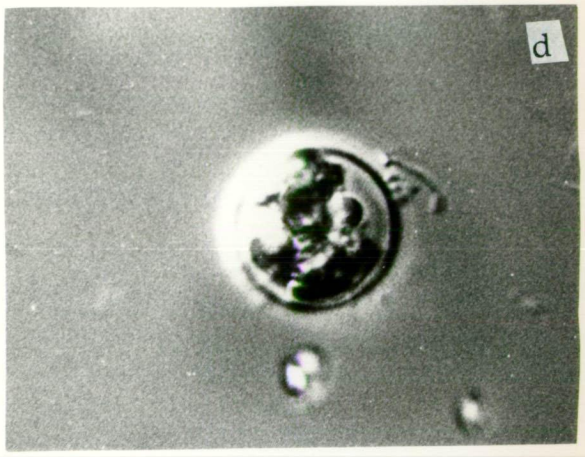


Plate 1.2a: P. gelidicola cyst scale distorted by sediment (200 x 400nm). b: P. gelidicola cyst scale with blunt projections. c: P. gelidicola cyst scale with knob and hook projections. d: P. gelidicola cyst (20 μm).

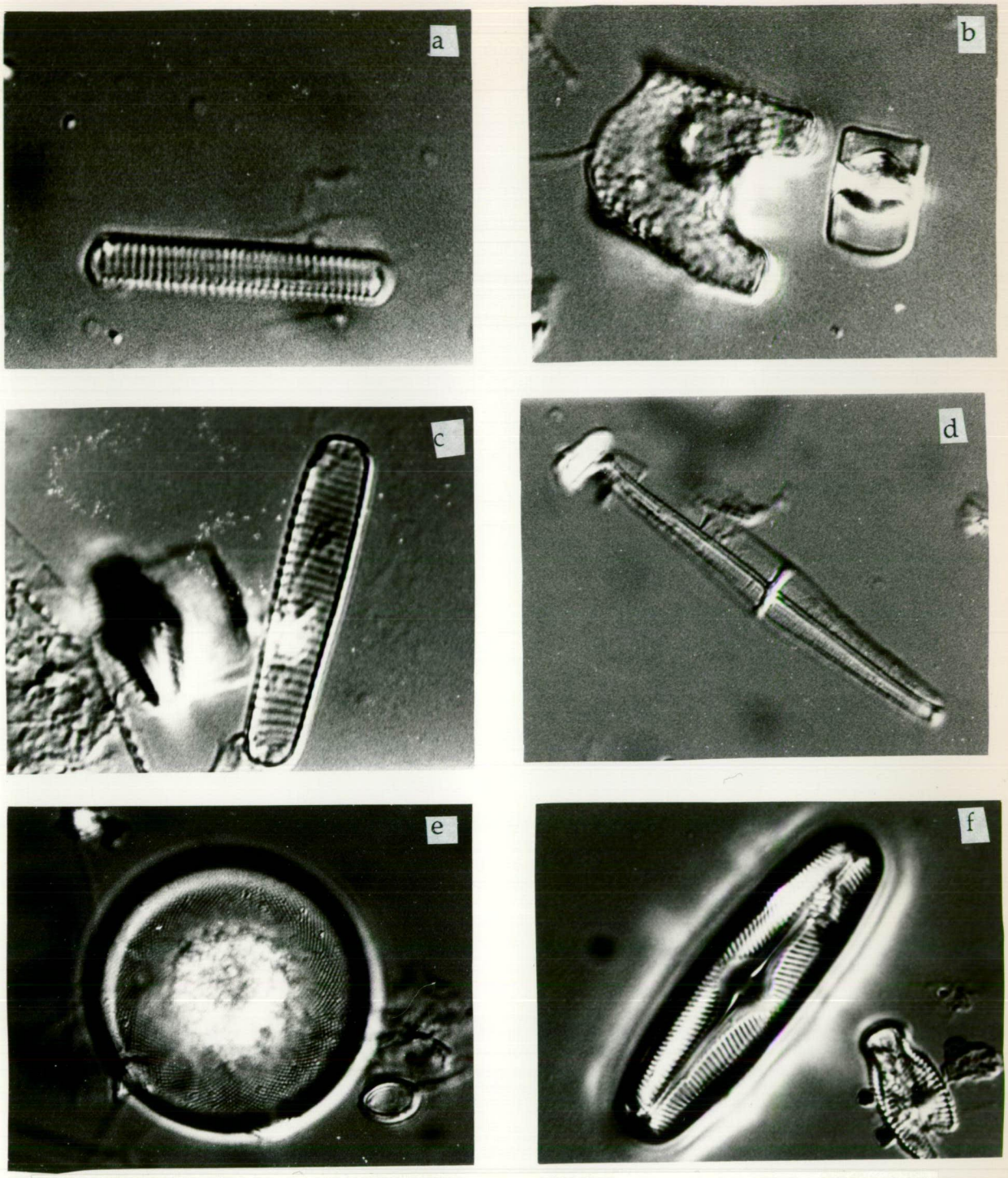


Plate 1.3a: Nitzschia cyclindrus (26µm). b: Eucampia antarctica (32µm). c: Nitzschia curta (26µm). d: Stauroneis sp. (44µm). e: Thallasiosira sp. (42µm). f: Pinnularia microstauron (64µm).

Chapter 2:

Controls on the growth and encystment of *Pyramimonas gelidicola.*

2.1 Introduction:

The Antarctic ecosystem supports a wide range of phytoplankton, many of which are potential climate indicators because they have a preservable record such as a resting stage, a hard exoskeleton or, as in Pyramimonas gelidicola's case, body and cyst scales. Very few of the phytoplankton in the Southern Ocean assemblage produce cysts or resting stages. The majority of the assemblage is made up of diatoms but, dinoflagellates, coccolithophorids, chrysophytes, prasinophytes and pymnesiophytes are also present. Diatoms and dinoflagellates are the most documented cyst producing organisms of the assemblage. However, with the exception of Thalassiosira, Eucampia, Odontella and Chaetoceros genera, very few cyst forming diatoms are found in Antarctic waters, because the sea ice diatoms in Antarctica are predominantly pennate (Hargraves *et al* ., 1983).

Dinoflagellates are not common in Antarctica and only one record has been found of the occurrence of resting spores in the sea ice of the Ross sea (Buck *et al.*, 1992). Diatoms have been known to produce cysts in response to nutrient stress or high salinities (Palmisano *et al.*, 1987, Doucette, 1989), and as nutrient levels are never limiting in Antarctica and low temperatures and light are the two main restrictions on growth, cyst production in the Southern ocean is not well understood. Whether diatom cysts are produced for the rapid dispersal of new genotypes or as resistant over wintering stages is unknown, therefore, the exoskeletons of diatom vegetative cells are the most commonly used palaeoclimatic tools. As diatoms are known to inhabit precise habitats which are governed by the chemical characteristics of the water column, the dominance of any particular genera or species of diatom is indicative of a particular environmental condition, such as hypersalinity or sea ice cover.

The growth of phytoplankton is usually controlled by light, temperature and nutrients such as nitrate, phosphate and silicate (Davies, 1990). In Antarctica, these main nutrients are not limiting, and their utilisation is limited by the low temperatures of the region (Riley and Chester, 1971, Warnke *et al.*, 1973). Low temperatures directly affect the growth rates of microalgae (Hawes, 1990). At low temperatures the photon flux saturation point is lowered and therefore, if high photosynthesis occurs, the extra carbon fixed will be converted into polysaccharide and lipid production instead of being utilised as protein (Morris et al., 1974, Hawes, 1990). This means that the growth rate of the species is independent of the photosynthetic rate. Morgan and Kallf (1975) determined that a decrease in nutrient concentrations will also lead to a decrease in growth rate and an increase in storage products. At the end of the summer bloom some ice algae have been reported to commence lipid production as a result of low nutrient concentrations (Priscu *et al.*, 1987). Hawes (1990) noted that blooms of Pyramimonas and other sea ice algae do occur when the ocean is covered in ice and light conditions are low. Carbon fixation is low, as is the photosynthetic rate but, as the optimum temperatures of the sea ice algae are also low, at 4°C the saturation point would be higher than in temperate species in similar conditions allowing for the full conversion of the photon flux to proteins and growth. In summer when light levels are

increased; polysaccharide storage increases perhaps in preparation for winter. The main growth season is spring in the sea ice zone, where light is not saturating. There has been little evidence in the literature that photoinhibition does occur in the Antarctic (Johnsen and Nost Hegseth, 1991).

Although in the marine environment low temperatures slow metabolism (Holm-Hansen *et al.*, 1977) sea ice and light restrictions are the main seasonal influences on the growth of sea ice algae (Everitt and Thomas, 1986). The sea ice algae of the polar regions are generally shade adapted (Bunt, 1964, Palmisano and Sullivan, 1982, Cota, 1985, Palmisano and Sullivan, 1985, Johnsen and Nost Hegseth, 1991), but, Rochet *et al.*, (1986) determined that the optimum irradiance for protein synthesis of the sea ice community of Hudsen Bay is higher than ambient irradiance. Incident light varies monthly with fog and cloud cover (Weddell Sea, Antarctic; March: 400-2000μE) and so the sea ice phytoplankton may adjust on a short term basis to irradiation variations (SooHoo *et al* ., 1987). Self shading from the algal mats that line the undersurface of the sea ice is a major consideration in the variation of ambient irradiance; Smith *et al.*, (1988) observed light saturated ice algae *in situ* , when the algal mats were only millimetres thick. Snow cover can also determine the distribution of algae under the ice because of shading (Tucker, 1983, Bunt and Lee, 1970). Light is greatly attenuated by sea ice and snow cover and therefore photosynthesis under ice is always light limited and never at maximum rates, and therefore productivity is low (Palmisano *et al.*, 1987).

This low productivity could be due to the low nutrient concentrations of the ice sea interface (Cota *et al.*, 1987, Cota and Sullivan 1990, Gosselin *et al.*, 1990). Recent work on the succession of the Ellis Fjord population have shown that the diatoms are the first to bloom early in the season, followed by various taxa including Cryptomonas and the last to bloom late in the season were P. gelidicola (McMinn *et al.*, in prep). This could be an oligotrophic succession, lead by a depletion of nutrients, similar to those that occur in the sea ice region. The ice sea interface is nutrient rich throughout the winter season because of low biological activity and brine drainage from seasonal ice formation. When light increases these nutrients

are utilised in the first summer diatom bloom, and as the sea ice melts, mixing in the water column occurs, replenishing the nutrients allowing for the summer diatom bloom. Vertical mixing of the water column also introduces new light variations to the sea ice microalgal population, ones which they must adapt to on daily time scales (Lizotte and Sullivan, 1991). The ability of the sea ice biota to adapt to not only seasonal but also daily light variations is important; as it enables these species to live in the water column and therefore, serve as a seed population for polar marine phytoplankton blooms (Lizotte and Sullivan, 1991).

The distribution and abundance of species in the sea ice community in the water column is regulated by the salinity of the waters (Poulin *et al* ., 1983). Salinity, like light and nutrients, is a limiting factor in phytoplankton growth, but when the light and temperature are within the species-specific optima, the phytoplankton can tolerate a broader range of salinities (Kirst, 1990). It has been found that genera like Nitzschia, which are generally associated with the sea ice, can survive a broad range of salinities from 11.5-34‰, but have lower growth rates at fresher salinities (Vargo *et al.*, 1986). Because of the formation of ice in the Antarctic environment, the salinities of the water column are subject to wide variations. Marine Antarctic phytoplankton contend with periods of brine drainage (<50‰), and periods of melt (3-20‰). These fluctuations are also pertinent to phytoplankton living in the closed lake systems of the Antarctic continent. P. gelidicola has been sampled throughout the water column of Ace Lake, but was found to only concentrate at 10m in summer when incident light is at it's maximum. At this depth the alga is growing in 24‰, whereas over the rest of the year the *in situ* salinity of P. gelidicola could vary between 15-34‰ (Burch, 1988). The ice cover in Ace Lake can be annual, so brine production is unpredictable and as the lake receives meltwater input (J. Gibson, pers comm.) the bottom layer of the lake is not hypersaline (34‰). The resident ice cover also decreases the irradiation input, daily and seasonally, into the lake. Burch (1988) measured the maximum incident light for Ace Lake in February as 1225 $\mu Em^{-2}s^{-1}$, and 1.3 $\mu Em^{-2}s^{-1}$ in July. At 5m depth in the lake the two readings were decreased to 245 $\mu Em^{-2}s^{-1}$ (ice free) and 0.03 $\mu Em^{-2}s^{-1}$ (1.2m Ice). At 10m the lake in summer has a maximum of 1% PAR (Burch, 1988). The temperature range at this depth is

6-8°C, but during the autumn and winter P. gelidicola is found through out the water column in a temperature range of -1-6°C (Burch, 1988). Therefore, it appears P. gelidicola has maximum growth in light conditions of 10 $\mu Em^{-2}s^{-1}$, 6-8°C and 24‰ during summer at 10m in Ace Lake.

Cysts of marine species of prasinophyceae are planktonic, photosynthetic and non motile (Belcher, 1970, 1968). The production of cysts by Pyramimonas has been observed since 1938 (Korshikov, 1938), but as yet the mechanism for cyst production has not been found. Cysts have been observed in P. pseudoparkae, P. parkae, P. gelidicola, P. tetrarhynchus, P. reticulata, P. amylifera and P. grossii (Korshikov, 1938, Parke, 1949, Parke *et al.*, 1965, Aken and Pienaar, 1981, McFadden *et al.*, 1982, Pienaar and Aken, 1985, van den Hoff *et al.*, 1989) although little is known of their composition or purpose. Comprehensive studies have only been carried out on the cysts of three species: P. amylifera, P. gelidicola, and P. pseudoparkae (Hargraves and Gardiner 1980, Pienaar and Aken 1985, van den Hoff *et al.*, 1989). The morphology of the cysts are variable; P. amylifera and P. gelidicola cysts have a scale covering (Hargraves and Gardiner, 1980, van den Hoff *et al.*, 1989), while those of P. pseudoparkae are scaleless (Pienaar and Aken, 1985). Light microscope studies of P. grossi, P. reticulata and P. tetrarhynchus (Belcher, 1969, Parke, 1949) show that they all adhere to sand grains but only the first two have a mucilage layer (Parke, 1949). As the cysts are non motile, the organic scales covering P. gelidicola cysts may have a twofold function as added protection to the cyst wall and an adhesive agent (van den Hoff *et al.*, 1989). This adhesive function could be an important reason for the preservation of the cyst scales in both marine and lacustrine environments.

In Antarctica, diatom frustules can be up to 60% of the sedimentary matter ($1x10^8$ frustules per gram of sediment) (Kozlova, 1966, Stockwell *et al.*, 1991). This is due to the dominance of the diatoms in the phytoplankton assemblage and the size and regularity of blooms. The most common diatoms in the sediments and water column of Prydz Bay are Nitzschia curta, N. cyclindrus and N. closterium (Stockwell *et al.*, 1991). The surface sediments of McMurdo Sound are dominated by Nitzschia also (Leventer and Dunbar, 1988). Their widespread dominance is the main reason that

Nitzschia are a common parameter used in palaeoclimatic studies, as well as the fact that a lot is known of the physiological tolerances and optima of these species. As these species are commonly epontic or associated with the sea ice, centric genera such as Thalassiosira, are often chosen as a comparison species because of their association with the open waters of the Antarctic ecosystem (Leventer and Dunbar, 1988). Another polar species, Eucampia antarctica, has two different varieties, one is sub-polar (E. antarctica var. antarctica) and the other is coastal (E. antarctica var. recta) (Fryxell 1991). So, the presence of the Antarctic convergence can be approximated in the past from records in the sediment and as E. antarctica var. recta produces differing winter and summer frustules, the temperature of the coastal waters can be estimated (Fryxell 1991). Past work has shown E. antarctica var. recta to be more abundant during periods of climatic cooling with increased sea ice cover, which makes the species an important tool in palaeoclimatic studies (Burckle and Cook, 1983). Comprehensive studies of the diatom stratigraphy of open ocean cores in Antarctica have been conducted to determine if climatic and oceanographic changes recorded in the northern polar region occurred in the southern polar region, and also to determine the fluctuations in the ice sheet over time. For example, by determining the proportion of sea ice and open ocean species in any particular section of a core, the investigator is able to determine if the sediment was laid down under sea ice or in the open ocean. This is much the same technique as used in the lakes of the Antarctic region. The species of diatoms in the lakes are restricted usually to pioneer/generalist species. Consequently, small physiochemical changes can go undetected in the stratigraphy of the lake due to the wide tolerance range of the resident species. Therefore, a technique that provides more detail of these parameters is necessary to be able to determine as much information as possible from these preserved data banks. If the mechanism of cyst production of a species such as Pyramimonas gelidicola was known, it could be more sensitive to climate changes than diatoms by using sediment records of both cyst occurrence and species presence and abundance in comparison with the changes in the diatom assemblage. This species is particularly robust and is found in most water systems in the Antarctic. Its presence in the continental lakes also means that it could be used to investigate the evolution of the

terrestrial systems since the Holocene deglaciation.

In order to determine the accuracy of using P. gelidicola scales as a climate indicator, it is necessary to determine the conditions in which the species survives, thrives and encysts. The purpose of this culture study was to determine the mechanisms that promote encystment in the species and to determine the correlation of optimal growth conditions and the promotion of encystment in two different strains of the species from different localities.

2.2 Materials and Method

Each of the growth experiments was carried out on two different strains of Pyramimonas gelidicola, an Ace Lake strain and a Prydz Bay strain. Both of these strains are maintained at the Antarctic Division, Kingston in $F/_2$ culture in 4°C and 65 $\mu Em^{-2}s^{-1}$. The two different strains were used in order to determine if there are any physiological differences between an Ace Lake strain as a representative of lake P. gelidicola and a Prydz Bay strain as a representative of marine P. gelidicola.

2.2.1 Media:

All of the growth experiments used artificial sea-water (32‰) as the standard culture medium. This medium was made up according to the Aquil formula of Morel *et al.*, (1979), which is specifically designed to cater for the requirements of marine phytoplankton growth. As these experiments didn't require the trace metal specificity of the Aquil formula, the salt content of the recipe was used and $F/_2$ medium used to supplement the trace nutrients and nutrients (Guillard and Ryther, 1962) (Fig 2.1). The $F/_2$ medium consists of 13 stock solutions, which allow for the testing of different nutrient and trace metal levels if required. Once the media were mixed they were filtered using a 0.2µ millipore filter and stored in the dark at 0°C.

Fig 2.1: Nutrient Concentration Table

	F/50	F/20	F/2	F	2F	Prydz Bay*	Ace Lake°
Nitrate							
NO3							
(g/L)	2.22E-03	5.44E-03	5.54E-02	1.11E-01	2.22E-01	9.96E-04	4.66-04
Phosphate							
PO4							
(g/L)	1.38E-04	3.45E-04	3.45E-03	6.90E-03	1.38E-02	1.28E-04	5.46-04
*Parker. N., (1992)							
°At 10m: (Burch, 1988)							

Fig 2.2: Modified Base Aquil Formula			
Salts:	gL^{-1}	Nutrients:	mlL^{-1}
NaCl	24.53	MnCl2.4H2O	0.5
$CaCl_2.H_2O$	1.54	Na2SiO3	0.5
KBr	0.1	$CoCl_2$	0.5
NaF	0.003	KH_2PO_4	0.5
KCl	0.7	$CuSO_4.5H_2O$	0.5
H_3BO_3	0.03	$ZnSO_4.7H_2O$	0.5
Na_2SO_4	4.09	$NaNO_3$	0.5
$NaHCO_3$	0.2	$NaMoO_4.2H_2O$	0.5
$SrCl_2.6H_2O$	0.017	Fe EDTA	0.5
$MgCl_2.6H_2O$	11.1	Biotin	0.5
		Citric Acid	0.5
		Thiamine	0.5
		B_{12}	0.5

2.2.2 Experimental techniques

•Temperature:

The Temperature experiments were all preformed in standard Aquil (32‰) and $F/_2$ medium. 10ml of this media was placed in three replicate 12ml Falcon culture tubes for each of the 20 temperature treatments. These tubes were inoculated with 1ml of the stock culture and then placed in a temperature gradient incubator. This experiment was carried out for a wide range of temperatures (-1.5. -0.5, 1.5, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18°C), and a continuous light source of 10 $\mu Em^{-2}\ s^{-1}$ for a period of 30-34 days until growth in all replicates had ceased.

• Salinity:

In the salinity experiments, the media concentrations used were 5, 10, 15, 20, 30, 35, 40, 50, 60, 75, 80, 85, 90, 100‰. These salinities were prepared by

adjusting a base Aquil solution of 100‰ with sterilised water. The $F/_2$ solutions were then added to the adjusted stock solutions to produce the final medium used in these experiments. For each of the 14 salinity experiments 30ml of the medium was placed in three replicate 50ml Falcon culture jars and inoculated with 3ml of stock culture. They were then placed on a light table consisting of two cool white fluorescent tubes giving a light intensity of 10 $\mu Em^{-2} s^{-1}$ and cultured in a controlled temperature room at 8°C for 30-54 days until growth in all replicates had ceased.

• Nutrients and Light:

The Nutrient experiment medium contained the standard Aquil seawater which had been adjusted using the $F/_2$ Stock solutions to give a variety of 5 different nitrate and phosphate concentrations: $F/_{50}$, $F/_{20}$, $F/_2$, F, 2F. All other nutrients and metals were kept at the standard $F/_2$ level (Fig2.1). As in the salinity experiments 30 ml of the media of the nutrient solutions was placed in three replicate 50 ml culture jars and inoculated with 3ml of stock culture for each of the five nutrient treatments. Three of these nutrient experiments were set one on each of three different light tables each providing 3, 10, 20 μEm^2s^{-1} respectively. The treatments were carried out at 8°C in a controlled temperature room for the period of 30-35 days until all replicates had ceased growth.

2.2.3 Sampling and Counting Techniques:

The concentration of cells and cysts were determined from five samplings of the stock cultures before inoculation of the treatments, which were enumerated using a haemocytometer. Once inoculated each of the three replicates were sampled and enumerated every two days. P.gelidicola cysts are known to affix themselves to the bottom of culture flasks (van den Hoff *et al.*, 1989), and so each of the flasks was shaken vigorously before sampling. Sampling involved extracting approximately 0.33 ml from each replicate and filling a Neumeyer Haemacytometer. The samples were fixed using a drop of Lugols solution and then the cells and cysts present counted on a Zeiss inverted microscope.

2.3 Results:

A 0.2 mm deep Haemacytometer with Neubauer ruling was used to enumerate the cultures. Species less than 75 µm will distribute evenly on the slide but it is useful for cell densities of more than 5×10^3 cells ml^{-1} (Guillard, 1978). Therefore, as the cell concentrations were an order of magnitude less than the lower limit, the errors of the majority of the data were over 10%. The errors decreased as cell concentration increased above 5×10^3 cells ml^{-1} for each of the treatments. Two parameters will be used to analyse the data; the maximum cell number and the cell growth rate. The maximum cell number is the peak cell concentration of the treatments, and the cell growth rate is a measurement of the exponential growth phase of the treatments only. The growth rates were calculated using the formula of Verity *et al.*, (1988).

$$K_{(doublings/day)} = Log_2(N_t - N_0 / t)$$

Where t= number of days of exponential growth.

N_t = no. cells at time t.

N_0 = no. cells at time 0.

2.3.1 Temperature:

The Prydz Bay Strain (PBS) of Pyramimonas gelidicola showed little response to changes in temperature over the broad range (-1°C - 10°C) at 32‰ (Fig 2.3). A slight increase in growth rate at 6-10°C was noted but is not significant. The cell numbers were low and the doubling rate 0.17 d/day (Fig 2.4). The Ace Lake strain (ALS) of P. gelidicola had a similar growth rate to the PBS except over the range of temperatures (6-10°C) when it increased by 50%. This high growth rate approx. 0.35 d/day, corresponded to increased maximum cell numbers which rapidly declined in direct proportion to the PBS at 10°C. The growth rates of the ALS indicated growth ceased at 18°C, while growth in the PBS ceased at 15°C.

2.3.2 Salinity:

The ALS experiment was performed first and because of the difference in growth rates of the Ace Lake strain after 50‰, a supplementary experiment was conducted to determine the growth of the species in 60‰

Fig 2.3a:

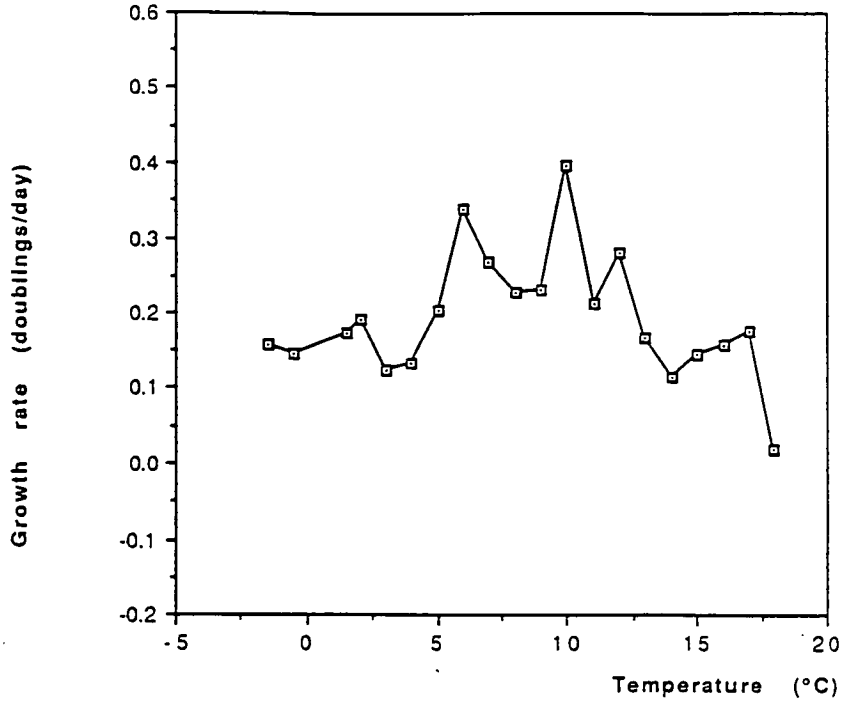


Fig 2.3b:

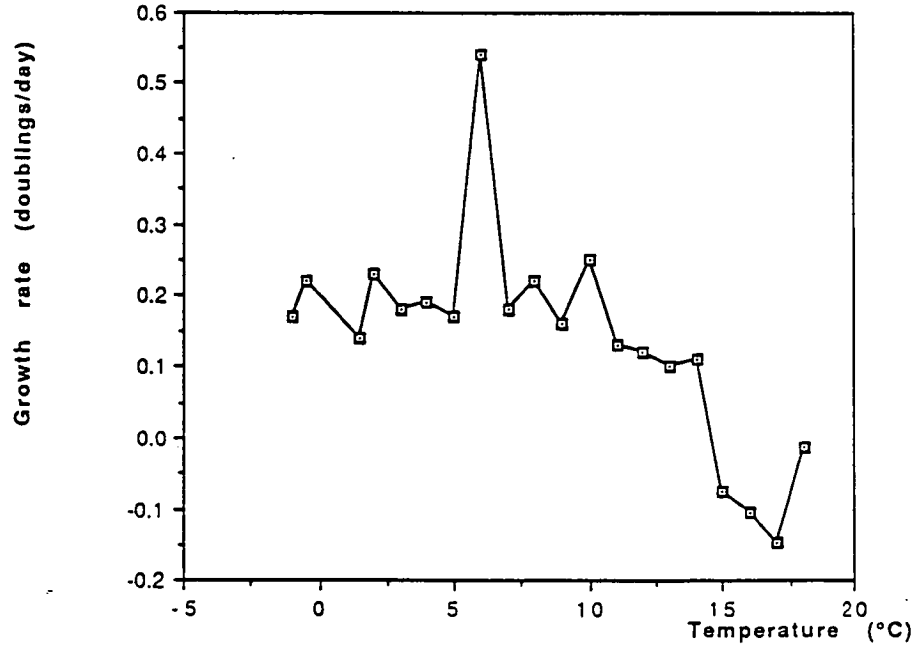


Fig 2.3: The cell growth rate of Ace Lake (2.3a) and Prydz Bay (2.3b) P. gelidicola when cultured in $F/_2$ medium at 32‰ and 10 $\mu E/m^2/s$ over a temperature range of -1.5- 18°C.

Fig 2.4

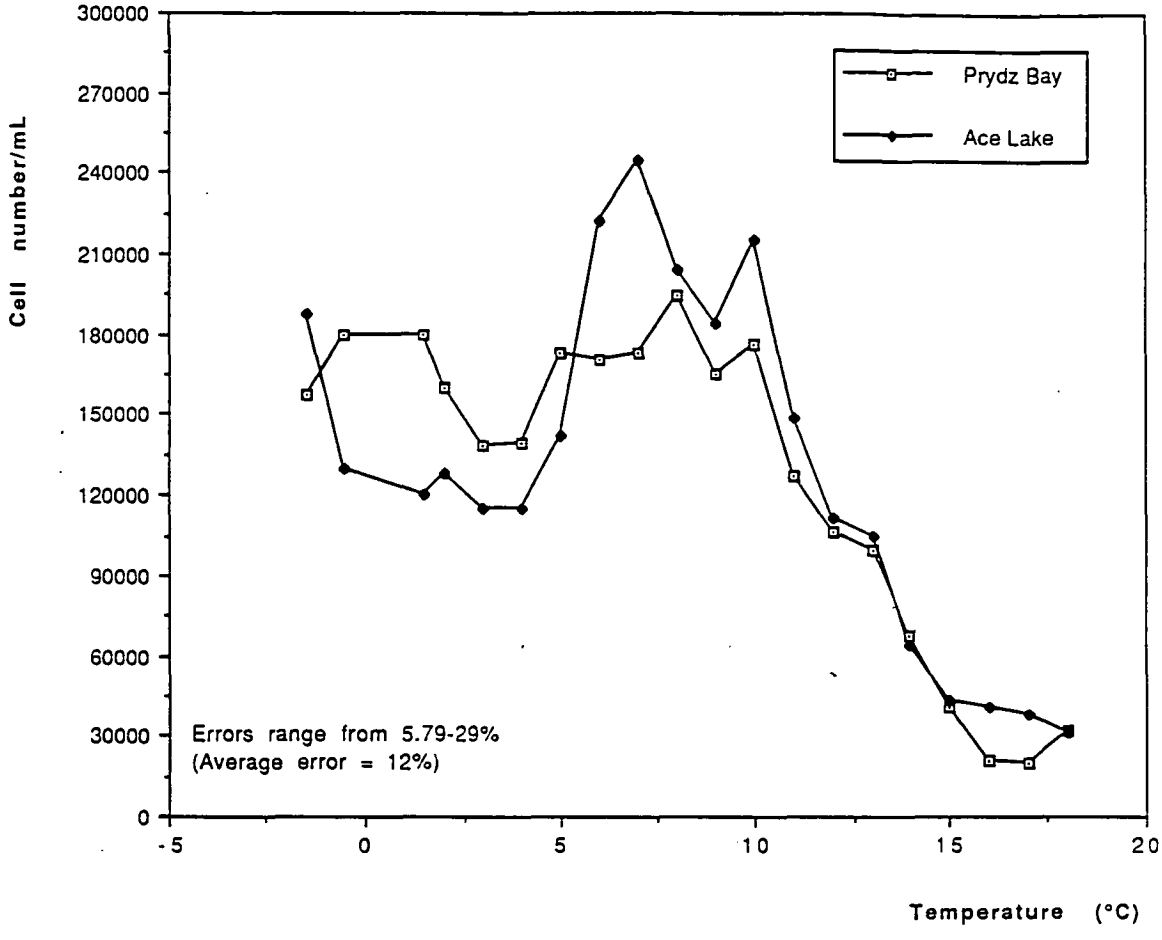


Fig 2.4: The maximum cell number of Ace Lake and Prydz Bay P. gelidicola when cultured in $F/_2$ medium at 32‰ and 10 $\mu E/m^2/s$ over a temperature range of -1.5- 18°C.

and incorporated with the results of the first experiment for comparison with the PBS experiment (Fig 2.5). The growth rates of both strains were constant until respective lethal salinities were reached (Fig 2.5). The optimal range of the ALS was between 30 -60‰. (Fig 2.6). Growth of this strain ceased between 80 -85‰. The PBS had a narrower optimal range of 60‰, with growth ceasing between 60 and 75‰. Both strains showed the ability to survive at lower salinities (5‰).

2.3.3 Light:

At 3 $\mu Em^{-2}s^{-1}$ the growth rates of both strains of algae were low (Fig 2.7), but growth was maintained for longer reaching higher maximum cell numbers (Fig 2.8). Higher growth rates were seen at 20 $\mu Em^{-2}s^{-1}$ for both strains, with only the PBS reaching higher cell numbers in higher nutrient levels. Growth rate and maximum cell number results are reciprocal at the standard nutrient concentration $F/_2$.

2.3.4 Nutrients:

The Prydz Bay strain showed a preference for higher nitrate and phosphate concentrations and a definite restriction at lower nitrate and phosphate levels (Fig 2.7). This was the opposite of the Ace Lake strain, which showed no ill effects at lower nutrient concentrations, had a peak growth rate at $F/_{20}$ concentrations and a maximum cell number at $F/_2$ (Fig 2.8). The optimum nitrate and phosphate concentration for growth, judged by the maximum cell numbers, for both strains was the recommended $F/_2$.

2.3.5 Cyst development:

P.gelidicola cysts are noted to affix themselves to the bottom of culture flasks (van den Hoff *et al.*, 1989). As a precaution the maximum cyst number per treatment was used in order to determine the treatments in which cyst production was greatest. In the nutrient experiments the maximum cyst number occurred for ALS within the optimum cell growth range, ie. treatments F and $F/_2$ (Fig 2.9) and fewer cysts occurred at higher and lower nutrients. The PBS produced an almost constant lower number of cysts than ALS with slight increases in the F and $F/_2$ treatments. The results for the salinity experiments show a marked increase in Ace Lake cyst production after optimum salinity for growth was passed and again

Fig 2.5a:

Fig 2.5b:

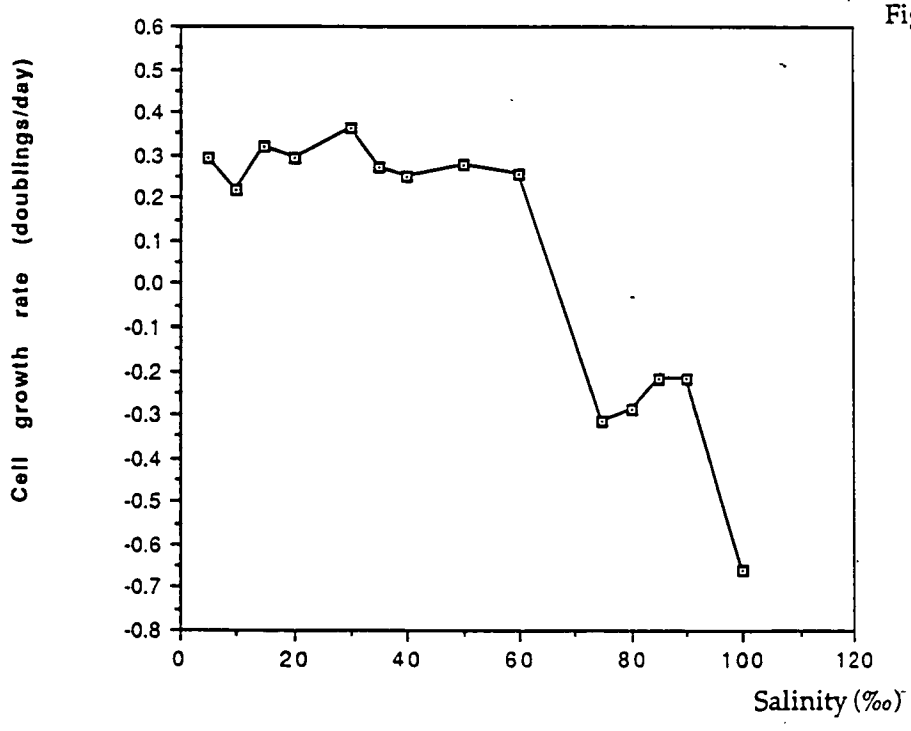


Fig 2.5: The cell growth rate of Ace Lake (2.5a) and Prydz Bay (2.5b) P. gelidicola when cultured in $F/_2$ medium at 8°C and 10 $\mu E/m^2/s$ over a salinity range of 5-100‰ .

Fig 2.6a

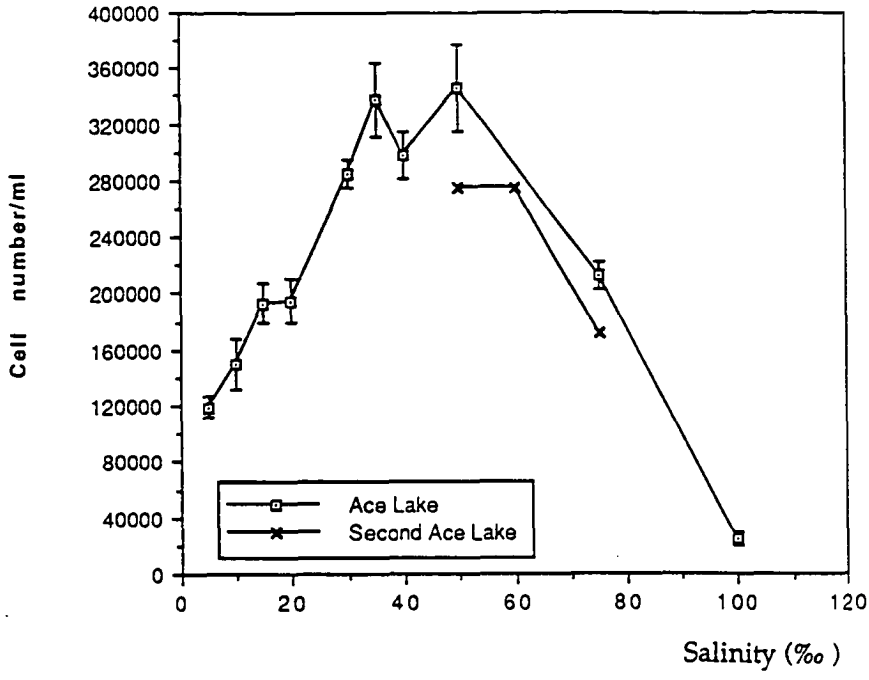


Fig 2.6b

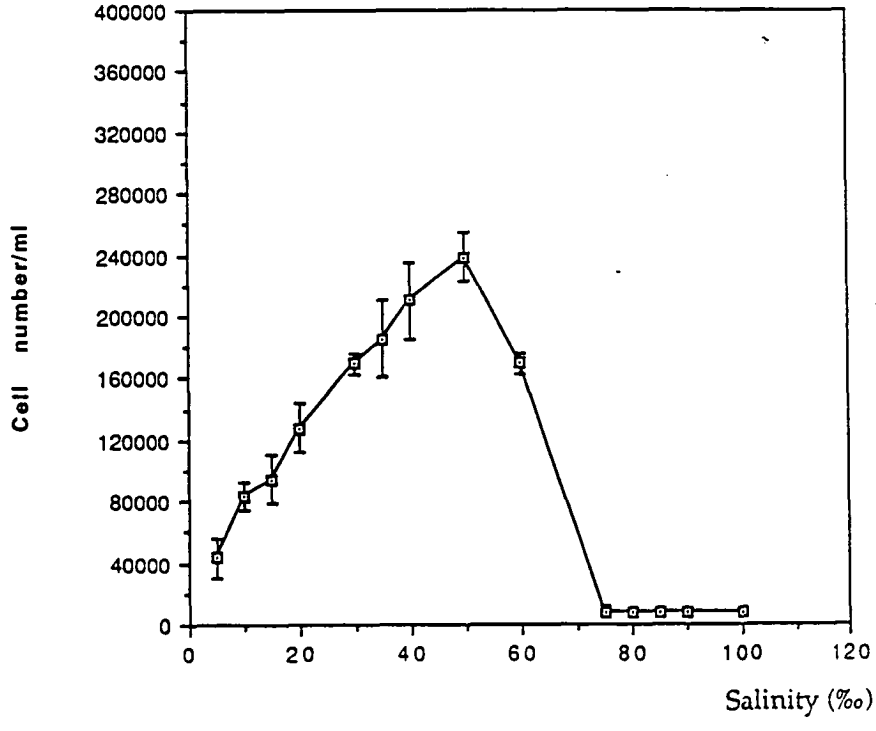


Fig 2.6: The maximum cell number of Ace Lake (2.6a) and Prydz Bay (2.6b) P. gelidicola when cultured in $F/_2$ medium at 8°C and 10 $\mu E/m^2/s$ over a salinity range of 5-100‰.

Fig 2.7a

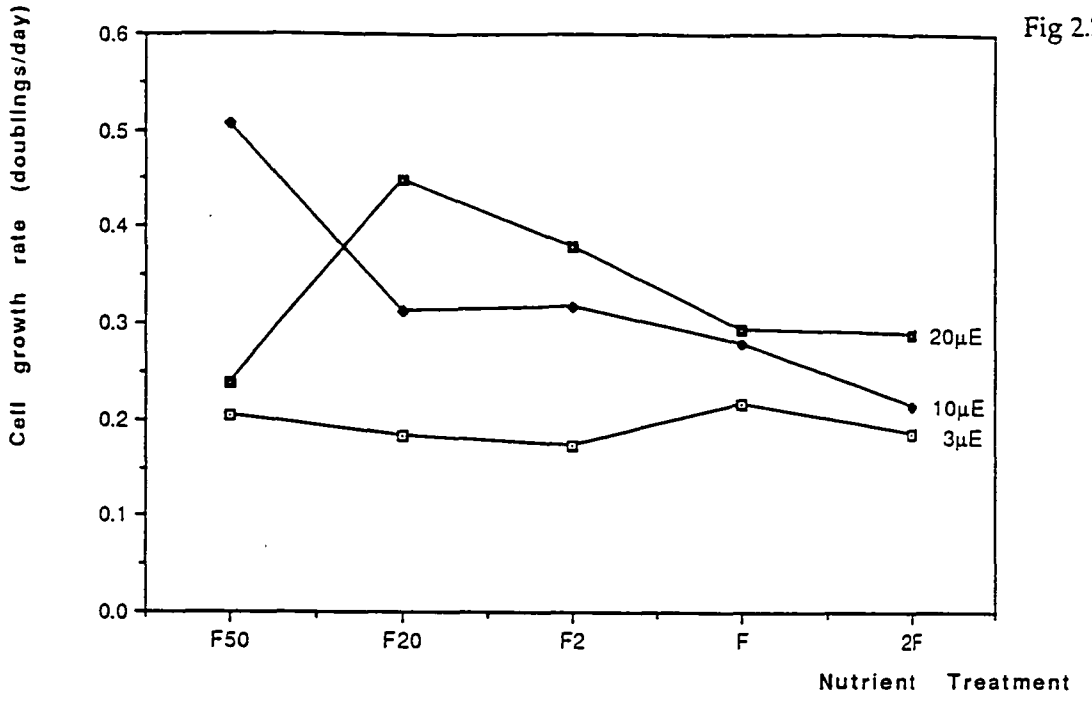


Fig 2.7b

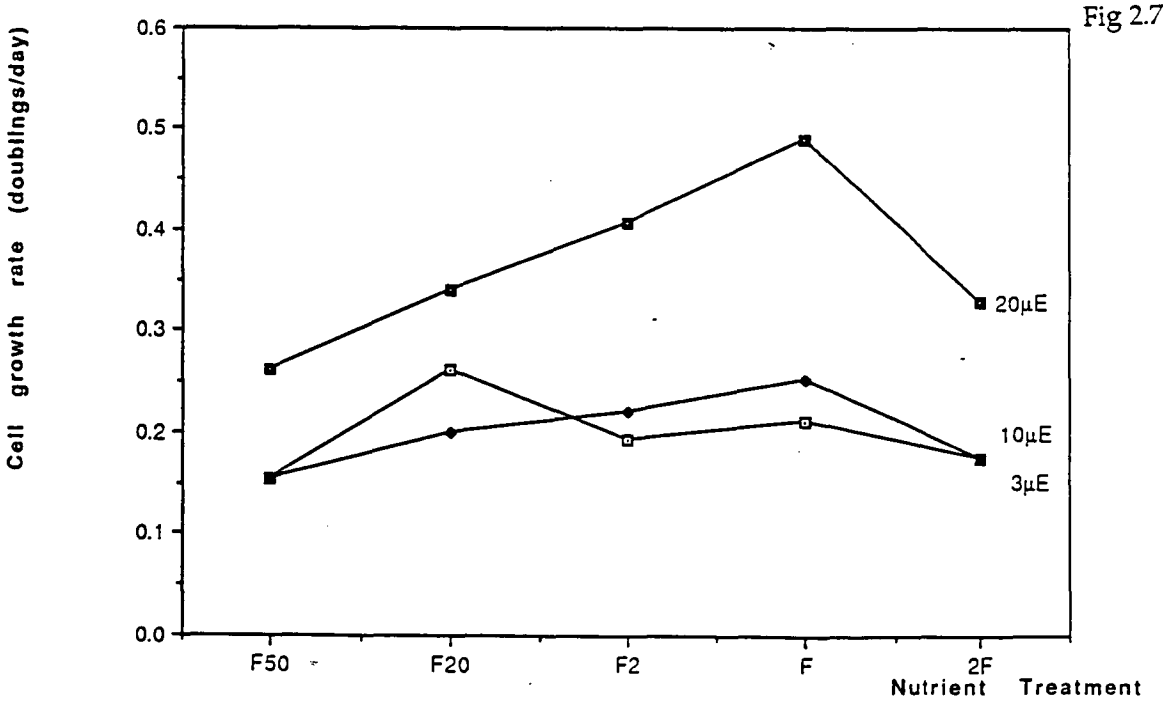


Fig 2.7: The cell growth rate of Ace Lake (2.7a) and Prydz bay (2.7b) P. gelidicola when cultured at 32‰ and 8°C over a nutrient range of $F/_{50}$-2F in light conditions of 3-20 $\mu E/m^2/s$.

Fig 2.8a

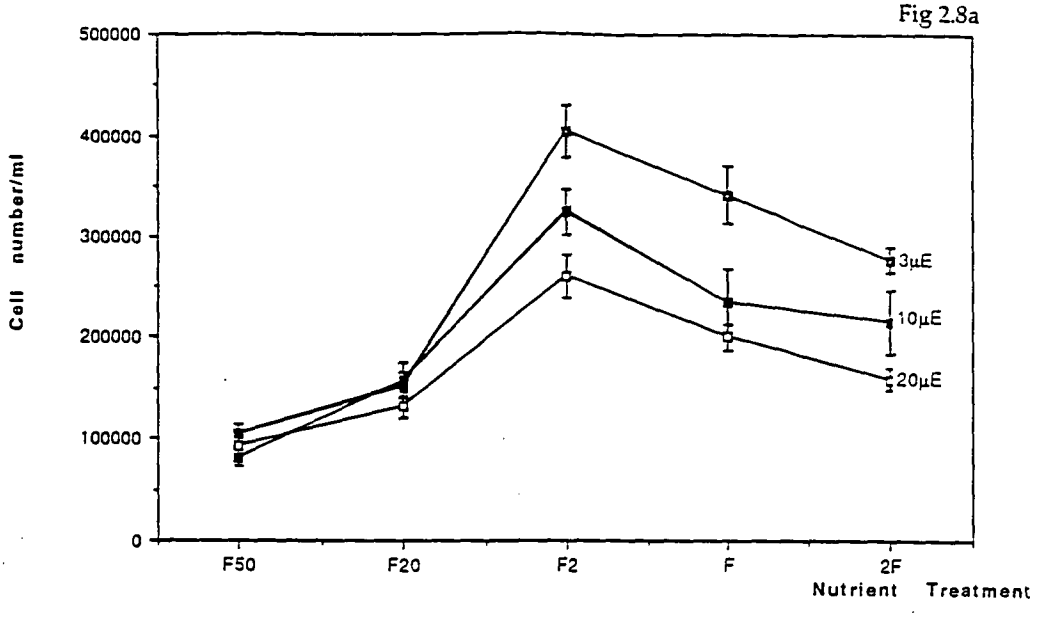


Fig 2.8b

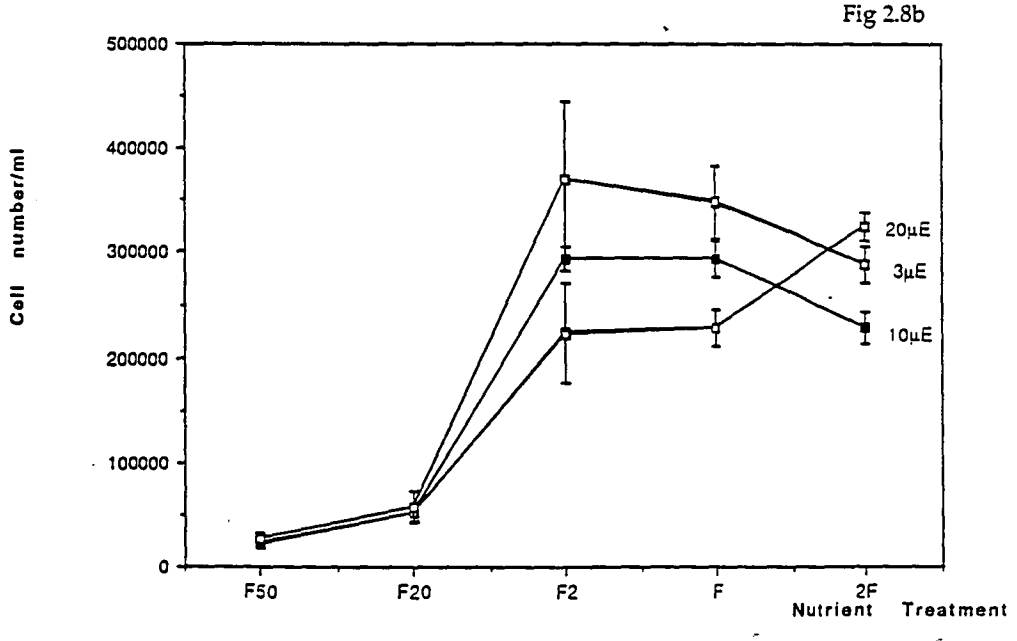


Fig 2.8: The maximum cell number of Ace Lake (2.8a) and Prydz bay (2.8b) P. gelidicola when cultured at 32‰ and 8°C over a nutrient range of $F/_{50}$-2F in light conditions of 3-20 $\mu E/m^2/s$.

Fig 2.9a:

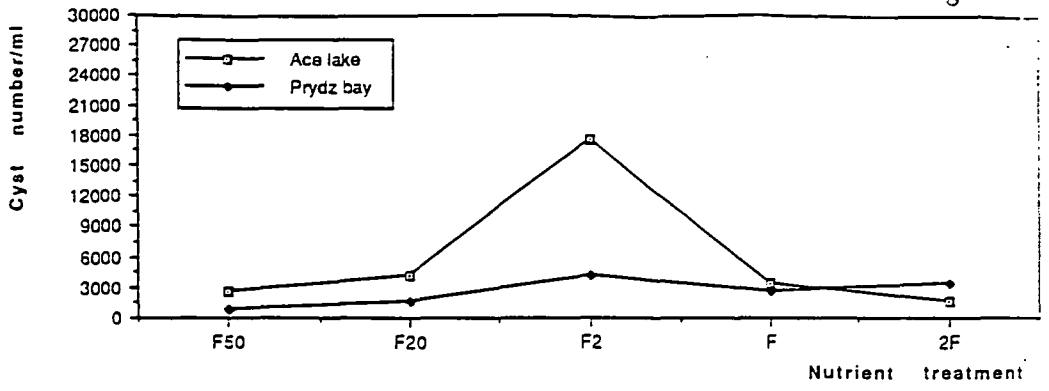


Fig 2.9b:

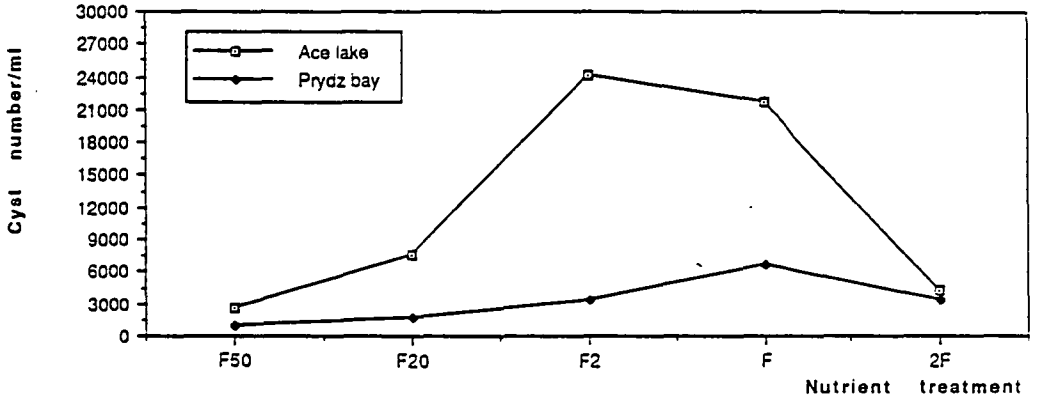


Fig 2.9c:

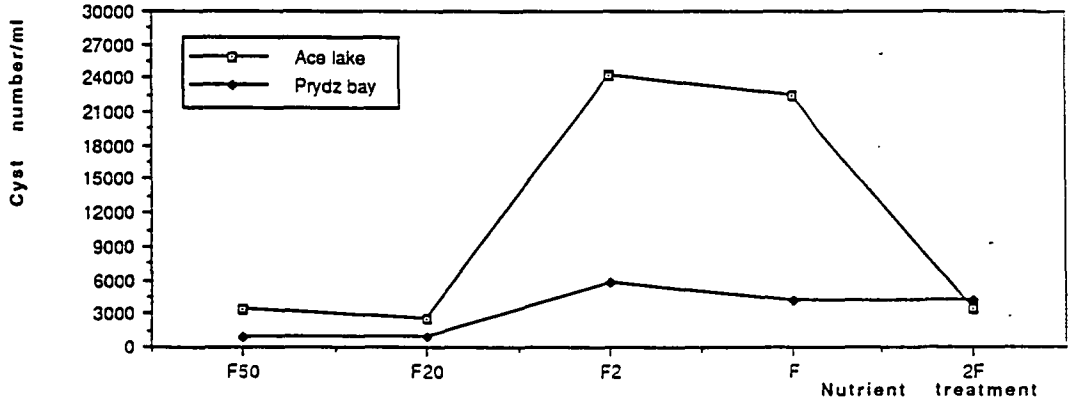


Fig 2.9: The maximum number of Ace Lake and Prydz bay P. gelidicola cysts when cultured at 32‰ and 8°C over a nutrient range of $F/_{50}$-2F in light conditions of 3 (2.9a), 10 (2.9b) and 20 (2.9c) $\mu E/m^2/s$.

there was a constant lower production of cysts by the PBS which followed no pattern (Fig 2.10). Temperatures above and below the optimum growth range (6-8°C) show a minor increase in cyst production in both cultures, but neither were significant, and overall the pattern with temperature is essentially random. Ace Lake produced at least 50% less cysts in this experiment (Fig 2.11).

There was also no indication of changing cyst production with growth phase (Fig 2.12). Cysts were produced in all treatments by both strains and no conclusive stress related production was noted.

2.4 Discussion

2.4.1 Temperature

Past studies of the Prydz Bay strain of P. gelidicola have shown that at 40 $\mu Mm^{-2}s^{-1}$, maximum photosynthesis occurs at 10°C (Mitchell, 1990). McFadden *et al.*, (1982) determined that the alga can grow in cultures at temperatures ranging from -2°C - 16°C. The species has been shown to still be motile at -10°C and it's flagella still beat at -14°C (Burch and Marchant, 1983). At these temperatures P. gelidicola keeps it's shape, unlike other species whose microtubules depolymerise at temperatures below 4°C. As the species does grow at 16°C it is unlikely that it produces an antifreeze product like other antarctic microalgae, such as Dunaliella sp., which produce the compounds to prevent nucleation, depolymerisation and freezing of their cytoplasm when in cold environmental conditions (Burch and Marchant, 1983). Therefore, P. gelidicola must be able to alter it's internal environment when cold stressed to maintain it's internal structure and consequently it's ability to divide.

This culture study indicates that P. gelidicola has an optimum temperature for growth of circa 7°C, indicating that it is a psychrophile (Morita, 1975). Previous work has shown that optimas for growth measured in culture are higher than they would be in situ (Smayda, 1969; Li *et al.*, 1980), therefore the optimum of P. gelidicola *in situ* could be less and similar to the optimas of sea ice diatoms (3-5°C) (Bunt, 1968; Kottmeier *et al.*, 1984). However, few sea ice diatoms can survive temperatures above the range of 6-9°C (Fiala and Oriol, 1990). Therefore P. gelidicola is not a true psychrophile,

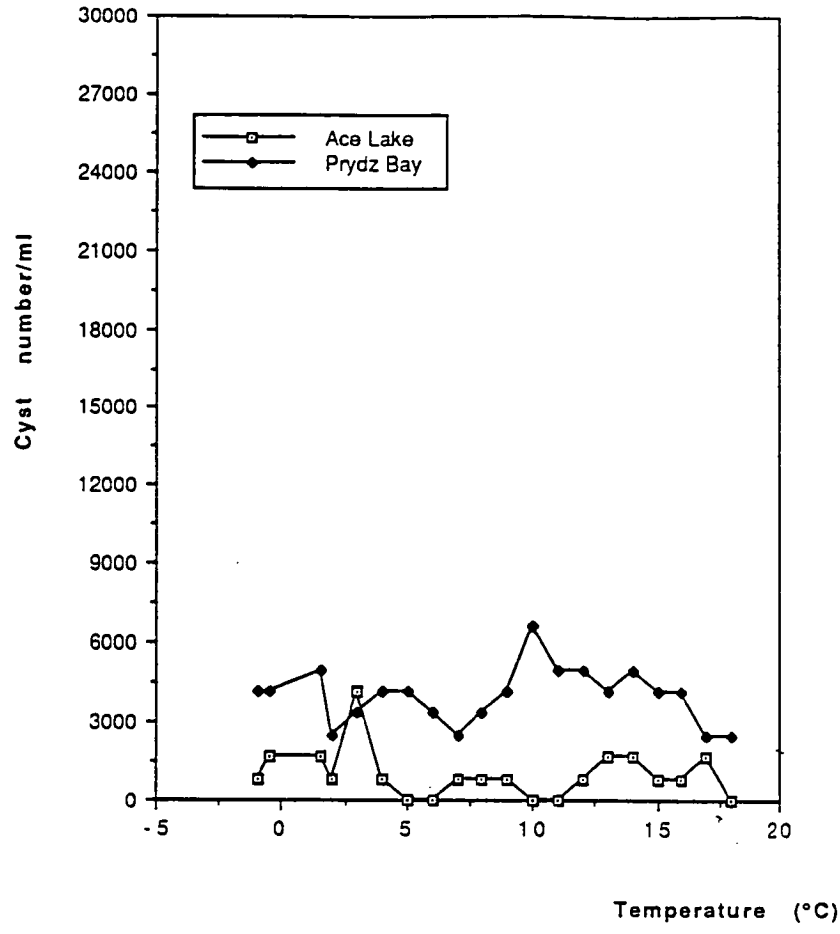


Fig 2.10: The maximum number of Ace Lake and Prydz Bay P. gelidicola cysts when cultured in $F/_2$ medium at 32‰ and 10 $\mu E/m^2/s$ over a temperature range of -1.5- 18°C.

Fig 2.11:

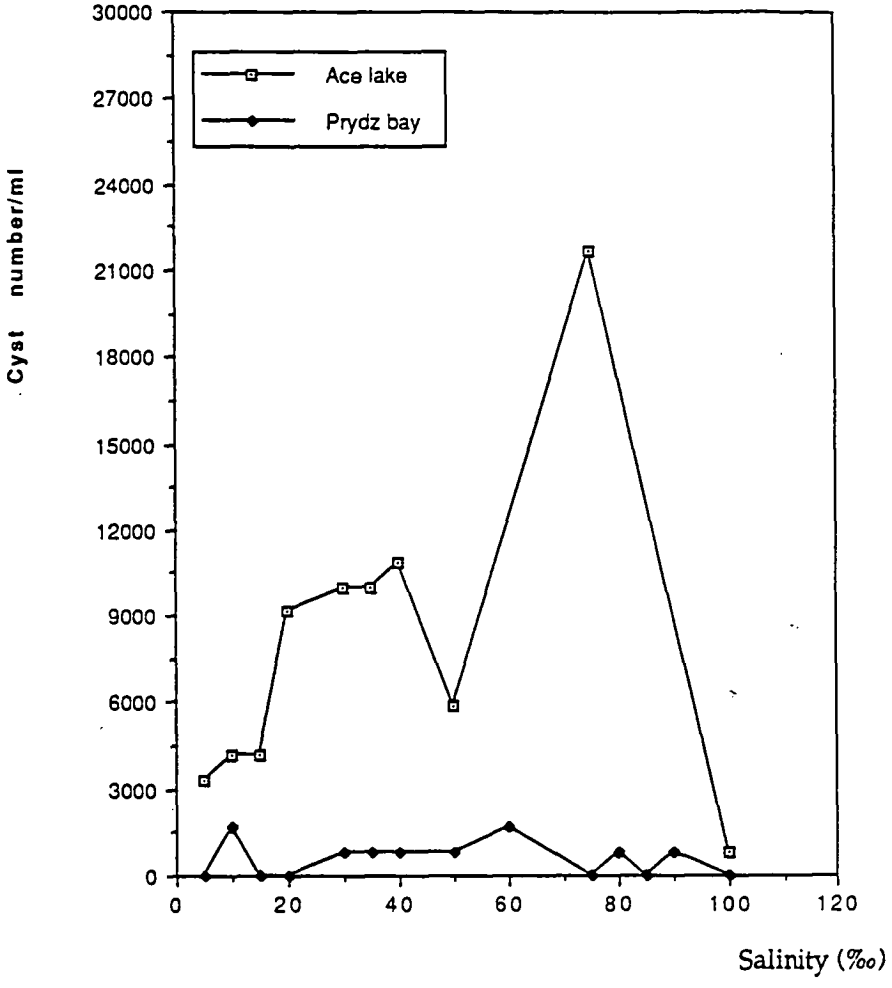


Fig 2.11: The maximum number of Ace Lake and Prydz Bay P. gelidicola cysts when cultured in $F/_2$ medium at 8°C and 10 $\mu E/m^2/s$ over a salinity range of 5-100‰ .

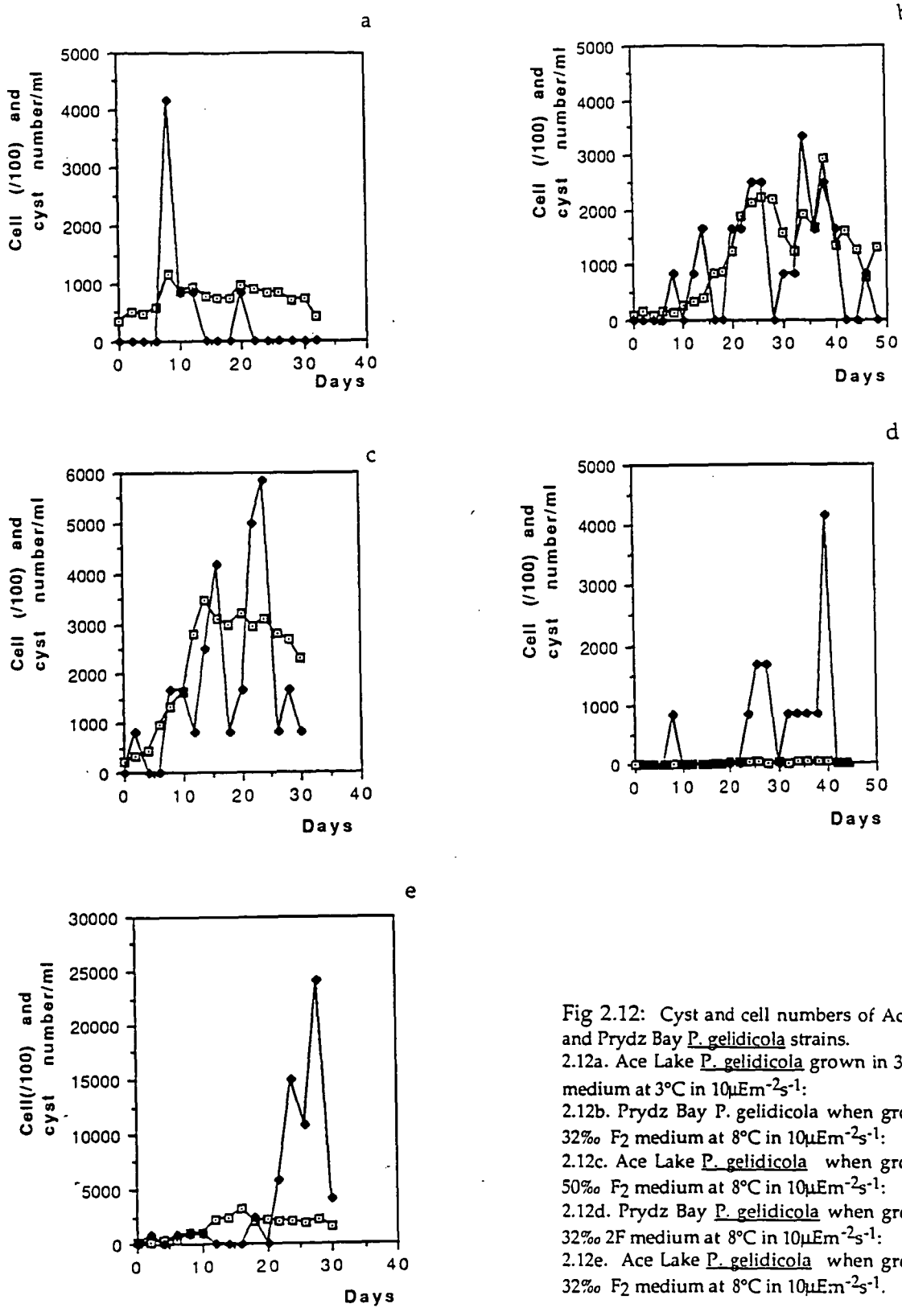


Fig 2.12: Cyst and cell numbers of Ace Lake and Prydz Bay P. gelidicola strains.
2.12a. Ace Lake P. gelidicola grown in 32‰ F_2 medium at 3°C in 10µEm^{-2}s^{-1}:
2.12b. Prydz Bay P. gelidicola when grown in 32‰ F_2 medium at 8°C in 10µEm^{-2}s^{-1}:
2.12c. Ace Lake P. gelidicola when grown in 50‰ F_2 medium at 8°C in 10µEm^{-2}s^{-1}:
2.12d. Prydz Bay P. gelidicola when grown in 32‰ 2F medium at 8°C in 10µEm^{-2}s^{-1}:
2.12e. Ace Lake P. gelidicola when grown in 32‰ F_2 medium at 8°C in 10µEm^{-2}s^{-1}.

because it grows in temperatures above 10°C. P. gelidicola is the not the only Pyramimonas sp. found in polar waters. However, the Arctic prasinophyte, P. nansenii Braarud, has had little research, and it's growth optimas are unknown (Schmarda, 1850). Culture experiments on a similar species, Pyramimonas amylifera, showed that it had a wide range of temperature tolerance with optimal growth at 10-15°C and a maximum temperature of 25°C (Gardiner and Hargraves, 1979). P. gelidicola is therefore unusual in the sea ice community of Antarctica because of it's wide temperature tolerance.

The difference in the growth patterns of the two strains with temperature could be due to the adaptation of the ALS to more diverse conditions encountered in lakes than the PBS finds in the sea ice environment. The more tolerant ALS is believed to have developed separately from the Prydz Bay strain for at least 8000 years in lake conditions (Pickard, 1986). At present the alga is found concentrated in the lake in the oxycline in summer and subsequently is not nutrient exhausted but is growing in light less than 1% of PAR (Burch, 1988). The temperature range at this depth is 6-8°C, but during the autumn and winter this species is found throughout the water column in a temperature range of -1-6°C (Burch, 1988). This means that the algae would often be in it's optimal temperature range (6-8°C) unlike the PBS, which is mostly associated with the ice edge in an annual temperature range of -1-4°C (Perrin, *et al.*, 1987). Blooms of P. gelidicola have been reported in the sea ice of McMurdo and incoastal Prydz Bay (Parker, 1992), on the edge of the sea ice late in the season this occurrence could be due to increased nutrients from of vertical mixing or decreased salinity caused by ice melt.

2.4.2 Salinity:

Results of the present study show the growth rates of P. gelidicola did not decrease with decreasing salinity; unlike other sea ice species that have been studied (Fiala and Oriol, 1990; Kirst, 1990, Vargo *et al.*, 1986) this species was extremely halotolerant, surviving over a broad range of salinities (5-75‰.). Bunt (1964) found an increase in Antarctic diatom photosynthesis with decreased salinities, which is not unusual for polar species; Arctic diatoms can survive salinities of 10-50 ‰ (Grant and

Horner, 1976). P. gelidicola has an optimal salinity of 35-60‰, when grown in optimal light and temperature conditions. Both strains showed rapid decrease in growth rates and maximum cell numbers above 75‰. In a normal marine environment this salinity would be rare and in hypersaline lakes, stratification usually enables the growth of algae at the surface (Anderson-31.8-132.3‰; Fletcher-50.3-81.1‰) (van den Hoff *et al.*, 1989). It could be the halotolerant nature of P. gelidicola that enables it to survive in numerous lakes of the Vestfold Hills, but the high salinity optimum of the species means that it would never be growing in optimal saline conditions in Ace Lake or the marine environment. The ability of the species to grow in salinities of at least 5‰, must ensure it can survive in most salinity environments encountered in the sea ice and lakes of Antarctica.

2.4.3 Light:

This ALS experiment showed a preference for its *in situ* light intensity, whilst the PBS experiment showed an optimum growth, although lower than ALS, at higher intensities (10 $\mu Em^{-2}s^{-1}$ and 20 $\mu Em^{-2}s^{-1}$ respectively) which it would be subjected to after sea ice melt and could be an indication of the strains ability to photoadapt to daily and seasonal light fluctuations. The ALS did show some retardation at the higher light intensity which could be representative of the species resident depth in Ace Lake during summer of 10m when conditions are ice free. Both strains showed their ability to grow under ice cover, with survival at a light source of 3 $\mu Em^{-2}s^{-1}$, indicating that they may be shade adapted like many of the Antarctic diatom species (Johnsen and Nost Hegseth, 1991). A transmitted light intensity of 20 $\mu Em^{-2}s^{-1}$ would be the maximum received by the Ace Lake strain due to it's presence in Ace Lake during summer at 10 m. However, the Prydz Bay strain would receive light intensities greater than 20 $\mu Em^{-2}s^{-1}$ during summer months and therfore, a higher light intensity treatment could be more accurate at determining any genetic difference between these two strains.

2.4.4 Nutrients:

Nutrients are rarely limiting in either Ace Lake or coastal Prydz Bay. During winter when the lakes are stratified P. gelidicola has been sampled

in the surface waters of Ace Lake where nutrient concentrations are lower (Burch, 1988). This could explain the ability for the ALS to grow better in low nutrient treatments than the Prydz Bay strain. Consequently, the Prydz Bay strain preferred the higher nutrient level (2F and F) to the $F/_2$-F growth optima of the ALS. The higher growth rates of ALS at lower nutrient concentrations and the higher growth rates of the PBS at higher nutrients treatments also confirm this preference. It is difficult to compare the growth of this species with the growth of other sea ice species in terms of nutrient preferences. However, as this species is usually the last to bloom in the spring/summer, it could be that it prefers more oligotrophic conditions than other flagellates like, Cryptomonas. Diatom succession in the fjords and coastal waters of the Antarctic continent could be silicate controlled and not nutrient controlled (McMinn *et al.*, in prep).

2.4.5 Cysts:

Cyst production in the temperature experiments was random for both strains suggesting that temperature does not effect the encystment. Cyst production in the Prydz Bay experiments was limited and mostly random, except in the nutrient experiments where the maximum cyst production of both strains occurred. The Ace Lake strain showed pronounced cyst production in the salinity and nutrient experiments. However, the experiments showed conflicting trends, suggesting that cysts were produced in conjunction with increased cell numbers in optimal nutrient conditions for growth, but also with a decrease in cell numbers in salinity stressed conditions. This differs from diatom cyst initiation, which occurs in nutrient poor and salinity stressed conditions (Doucette, 1989, Palmisano *et al.*, 1987). The salinity results are not terribly conclusive because of the one point peak, which if ignored shows a random pattern of cyst production as seen in the temperature results. However, as the cysts were produced in greater numbers it is likely that salinity does affect cyst production and further testing necessary. The only conclusive encystment result was in the nutrient treatments and so it could be that P. gelidicola produces cysts as part of it's life cycle and not in response to poor conditions. However, daylength was not tested as a possible initiator of encystment, and if encystment is a mechanism of overwintering than daylength would be the a conclusive experiment to test the hypothesis.

If cysts are produced at the time of maximum cell concentration then the cyst could be a sexual stage which is produced for the rapid dispersal of new genotypes, instead of a cell that is able to withstand harsh conditions. This would be similar to diatom cyst production (Lee, 1980). However there has been no confirmed report of sexual reproduction in prasinophyte species. P. amylifera, P. parkae and P. pseudoparkae produce biflagellates from their cysts which could be zoospores, but further research is needed (Hargraves and Gardiner, 1980, Aken and Pienaar, 1981, Pienaar and Aken, 1985). Biflagellates were noted in this study, but no cyst was found containing them, and no empty cysts were observed. The germination time of the cysts may indicate their function. If a cyst has thin walls and germinates quickly then it could be a sexual stage more so than an armoured cyst. P. pseudoparkae and P. parkae, have no scale covering on their cysts unlike P. gelidicola and therefore they are not very resistant and are possibly a sexual stage. Whilst P. amylifera did germinate in the course of a month long experiment, it does have scales that are embedded in the matrix that covers its cysts. Belcher, (1970), studied two freshwater Pyramimonas species; P. reticulata and P. tetrarhynchus, that do produce scale covered cysts and found that neither cyst was resistant to desiccation or temperature. Therefore, cyst scales are no indication of the cyst's hardiness, or function. Further study is necessary to determine if the cysts produced by P. gelidicola are sexual stages and also to determine why there is such a close link between both the ALS and PBS cyst production in optimal nutrient conditions.

2.5 Conclusions:

Culture studies of Pyramimonas gelidicola under varying conditions showed that the Antarctic Lake strain had a broad tolerance of low light (3-10 $\mu Em^{-2}s^{-1}$), temperature (6-8°C) and salinity (35-60‰). The Prydz Bay strain did show broad tolerances as well, but this strain was not as halotolerant or oligotrophic as the Ace Lake strain. The Prydz Bay strain preferred higher light (20 $\mu Em^{-2}s^{-1}$) and nutrient levels (2F), had an optimum salinity of 60‰ and no temperature response below 10°C. Both strains grew at 5‰, -1.5°C, and 3 $\mu Em^{-2}s^{-1}$). The Prydz Bay strain ceased growth at 75‰ and 15°C, the Ace Lake strain ceased at 80‰ and 18°C.

The wide tolerances of the species and it's subsequent robustness, have enabled it to dominate the lakes of the Antarctic continent and to survive and bloom in the sea ice communities of Prydz Bay. As with any culture experiments the differences in the growth of two strains could be different from *in situ* reactions.

Cyst production occurred in all treatments in these experiments. In both strains the production was enhanced in the respective optimal nutrient conditions. The Ace Lake strain showed greater cyst production than the Prydz Bay strain in the salinity experiments but the results were inconclusive. Cyst production in the temperature experiments was random and greatly reduced, therefore temperature has no effect on the initiation of cyst production in P. gelidicola.

Cyst could be a sexual stage of the P. gelidicola life cycle, but the cysts have never been germinated. It is suggested that cyst formation is nutrient initiated and that a further study of salinity and daylength is important.

Chapter 3:

An examination of the Evolution of Ace Lake from a Sediment Core

3.1 Introduction:

Ace Lake is situated on Long Peninsula, in the Vestfold Hills (Fig 1.1). It was chosen for a palaeoclimatic study because it is a considerable distance from Davis Station, decreasing the possibility of anthropogenic input and also because it has been extensively studied since 1978. The lake contains a limited assemblage of flora and fauna, comprising Pyramimonas gelidicola, Cryptomonas sp., and two unidentified species, a microflagellate and an unarmoured dinoflagellate (Burch, 1988). Specimens of the diatom genera, Nitzschia and Navicula have also been sampled in the water column intermittantly and are proposed to be associated with the benthic mats that cluster the edge of the lake (Burch, 1988). Only one zooplankton has been confirmed to exist in the lake, Paralabidocera antarctica and therefore grazing is probably not a major restriction on biomass (Volkman *et al.*, 1986). Ace Lake's suitability for palaeoclimatic research rests on these factors: it is free from external

contaminations, it is a closed meromictic system with a limited biota and has been monitored extensively for last 24 years.

Ace Lake is believed to have been first formed when the Antarctic ice cap retreated 7-8000 years ago (Adamson and Pickard, 1986a). Abundant fossils of extant mosses and lichens and the ventifacts and straie of the rocks of the Vestfold Hills suggest that the climate and wind direction of the region have been constant since the last ice retreat in the early Holocene (Pickard *et al.*, 1986, Pickard, 1983). Climate records of the region have been collected since 1957 from Davis Station until present, excluding the period Nov., 1964- Feb., 1969, when the station was closed. Palaeoecological studies have been carried out in numerous lakes in the region as well as in Ellis Fjord and Tayanna Bay, (Burton and Barker, 1978, Pickard *et al*, 1986, Volkman *et al.*, 1986, Bird *et al.*, 1991, Bronge, 1992, , Mancuso, *et al.*, 1992). These studies included sulphur isotope measurements, fossil dating, lipid examinations, and sediment core analyses.

Diatom composition is a widely applied palaeoecological tool used to determine the evolution of any particular lakes or the climate change of a region but it has not yet been used in the Vestfold Hills area. Diatom analysis of sediment cores have been used extensively in Prydz Bay and other marine areas of Antarctica and the species that occur at certain temperatures and geographical areas are well established (Leventer and Dunbar, 1988, Fryxell, 1989). Wasell and Hakansson (1992) studied the diatoms in a sediment core from Squa Lake on Horseshoe Island, off the Antarctic Peninsula. From this work they were able to determine the changes in the diatom assemblage of the lake that represented brackish, marine and fresh lake waters. Changes in the regional climate of the area that occurred since the lake was formed were not evident from his data because the lake diatoms had very broad growth optimas.

These results prompted the search for a palaeoclimatic tool for lacustrine environments which were the focus of the work in Chapter 2. An Ace Lake sediment core was chosen as a test case to determine the implications

of Pyramimonas gelidicola vegetative and body scales as climatic indicators.

Examinations of the sediments of Ace Lake have been carried out by numerous researchers over the past 13 years, but no work has been done on the diatom stratigraphy of the lake. Burton and Barker (1978) suggested that there were three different stages in the lake's development based on their examination of the sulphur isotopes of the Ace Lake water column. The first phase included several cycles of mixing and meromixis, with most of the seawater being replaced by fresh and 76% of the sulphur disappearing from the system through biological reduction in the monimolimnion. This phase was followed by a phase of complete mixing which involved the replenishment of the sulphur concentrations. The final stage is present day meromixis when the local freshwater was layered on the older water left after the general circulation. They believed that this second meromixis was introduced by a second climate change and that it was maintained by the ice cover and the thermal and chemical stratification of the lake.

These stages were confirmed by Bird *et al*, (1991), through their physical analysis of an Ace Lake sediment core. They examined; C^{14} for dating, $\partial^{13}C$, sulphur and organic carbon (Fig. 3.1). By visual inspection they divided the core into three separate units:

•Unit One: 0-35 cms: Black, reddish black laminated algal material with occasional light carbonate rich bands (<0.5 mm).
•Unit Two: 35-130 cms: Diffusely banded watery green sediment, which changed over the bottom 5 cm to sediment similar to Unit 1.
•Unit three: 130-185 cms: The top 15 cms was similar to Unit One changing to grey laminated algal material with a decrease in laminations down the core as the proportion of fine clastic material increase. 170-180 cms had very little macroscopic algal material and the sediment was predominantly grey silt-sized clastic material.

Bird *et al.*, (1991) concluded that the sediments of unit two were probably marine in origin, and that the algal mats of units one and three were

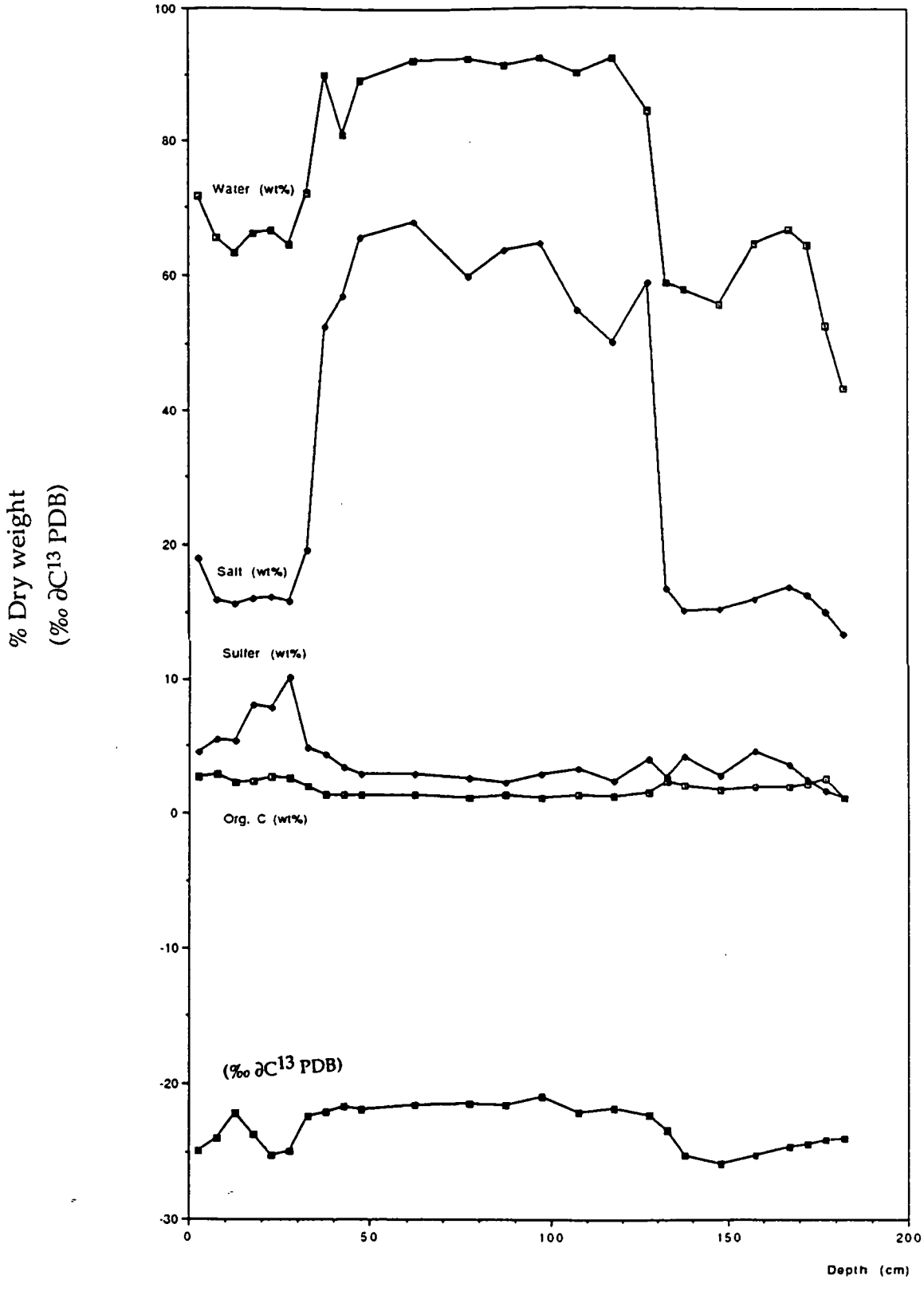


Fig 3.1: Physical parameters of an Ace Lake sediment core with sample depth. Note increase in water and salt content from 25-135 cm may indicate a marine influence. (after Bird etal., 1991)

similar to the description of those found in Highway lake and in the Antarctic Dry Valley lakes (Wharton *et al* ., 1983).

Bird *et al.*, (1991) determined the age of the sediments in Ace Lake by C^{14} dating. Carbon dating in Antarctica is subject to an inbuilt error of 1000-1500 years , which is a result of low concentrations of C^{14} in the Southern Ocean waters caused by the upwelling of old bottom water and the input of C^{14} depleted glacial melt water (Ohmoto, 1983). They dated 2 sediment levels in the core, one at the Unit 1-2 transition and the other in the middle of Unit 2 (20-35 cms; 35-75 cms). The dates were 5310±90 years before present and 6110±180 years B.P. respectively (uncorrected ages with the present being 1950). The sedimentation rate of the top 35 cms of the core is 0.06-0.08 mm/year, assuming a correction of between 0 and 1000 years (Bird *et al.*, 1991). Note that due to the low carbon content of the core, large amounts of sediment were needed to obtain a date, making the ages quoted above the average of a large time slice. The dated samples straddle sediment units 1-2 and therefore, the period of change in the lake from oxic to annoxic conditions. The rate of emergence of the lake is calculated as 1.6- 2 mm/yr (Bird *et al.*, 1991).

The sedimentation rates in Ace Lake are similar to those reported by Zhang *et al.*, (1983) and Peterson *et al.*, (1988), but are much higher than the rates calculated by Adamson and Pickard (1986b). The latter determined that the lake must have been ice free 8000 years ago, implying a much higher sedimentation rate in the past. It could be expected that after ice sheet retreat more sediment and glacial dust would have been present increasing the sedimentation rate. At that time the majority of the sediment would have been deposited into the lake via the same processes occurring today, a combination of fresh water run off, aerosols and sea spray. Pickard *et al.*, (1986), concluded in their study of the geomorphology of the Vestfold Hills that the climate there has been constant over the past 8000 years, as have the climates of Macquaire Island, Marion Island and St Georgia. Consequently, the net run off and precipitation entering the lake system would be constant, and the sediment rates of the lake would have been altered by melt water sediment loads. Results from other studies indicate that a marine episode affecting a lake,

(eg. washover or incursion), could also result in increased sediment input. Ellis Fjord shows a sedimentation rate of 2 mm/year (Bird *et al.*, 1991). The calculation of sedimentation rates can also be affected by compaction of the core during coring, or the loss of the uppermost portion of the core (Bronge, 1989). Therefore, sedimentation rates are often incomparable between other lake studies. Nonetheless, the sedimentation rates for the Ace Lake core used in this study fit in well with other sedimentation rates in the area.

Marine and lacustrine phases in a lake can be identified using the $\partial^{13}C$ values of the organic carbon in a sediment core to differentiate between high and low productivity when used in conjunction with organic carbon content (Bird *et al.*, 1991). Fluctuating $\partial^{13}C$ values (-29‰ to 10‰) are indicative of a lacustrine environment, whereas a marine environment has more constant $\partial^{13}C$ values (circa. -22‰) and usually a lower organic content. Potentially, $\partial^{13}C$ values of open marine sediments are heavier than those in an area which is subject to isostatic change forming a marine inlet; Ellis Fjord has $\partial^{13}C$ values of -18‰. There are three ways to account for the decrease in $\partial^{13}C$ values when an inlet is formed: Heavy CO_2 produced in bacterial fermentation in the deeper waters has been utilised by planktonic microbes in the bottom waters; The poor circulation of the inlet and increased plankton populations in summer reduce pCO_2 in the surface waters thereby decreasing the isotopic fractionation exerted by the microbial population during photosynthesis (Calder and Parker, 1973; Pardue *et al* ., 1976): Lastly the comparatively warm bottom temperatures of an inlet (up to 2°C) result in a decrease in the magnitude of fractionation (Bird *et al* .,1991). The $\partial^{13}C$ data from Ace Lake, proved to be inconclusive because the organic content of the core was constant for most of the samples and did not correlate with the changes in the $\partial^{13}C$ values.

The change from a marine environment to a marine inlet can be identified from the sediment record by examining the diatom assemblage of a core for an increase in the concentration of pioneer species, or by identifying an increase in sulphur content of the core. Bird *et al.*, (1991), found sulphur present throughout the core, perhaps indicating some anoxic bottom waters were always present in the lake. Units 1 and 3 were interpreted as

meromictic because of their high sulphur concentrations and low $\partial^{13}C$ values. Increased sulphur content in the transition from unit 2 to unit 1 are inversely proportional to the $\partial^{13}C$ values indicating that unit 1 is anoxic. The high $\partial^{13}C$, low sulphur and constant organic carbon trends of unit 2 suggest that the conditions of the lake at this time were stable and oxic. This would usually indicate a marine environment. Without a detailed investigation of the microfossil stratigraphy of the sediments however, the origin of the sediments of unit 3 were inconclusive because they did not have the characteristics of marine origin as seen in unit 2.

Bird et al., (1991) noted that whilst the sediments in section 2 of the Ace Lake core had marine charateristics, those of Unit One and Three did not. Therefore if unit Two was marine; the origin of unit Three was difficult to interpret, based on the weight of the sedimentological evidence. They therefore hypothesised that Ace Lake contained no marine sediments, and that all sediments in the core were lacustrine in origin. This conclusion agreed with that put forward for the evolution of the lake by Burton and Barker (1978), who determined, using sulphur isotopes that the lake had three phases of development. The first phase had both mixed and meromictic episodes, the second was holomictic, and the third was the present day meromixis. Burton and Barker (1978) suggested that a second climate change had occurred in order to induce the second stage of meromixis but they were unable to discern what type of change. These results corrolate well with the work of Volkman *et al.*, (1986), who determined using hydrocarbon analysis that the lake developed it's permanent anoxic basin only in the last 1000 years, and that before this time the depositional environment of the lake varied dramatically.

The intent of this study was to plot the evolution of Ace Lake since the retreat of the continental ice sheet by examining the changes in the scale and diatom assemblages preserved in the lake's sediments. By observing the presence and absence of the P. gelidicola cyst scales in relation to the body scales in the sediment core it was hoped local climate changes could be determined. In order to establish the accuracy of the scales for recording climatic change their abundances were compared down core with the diatom stratigraphy of the sediment core.

3.2 Materials and Method:

The core that was used in this study is the same core used by Bird *et al.*, (1991). It was collected in 1978 through the ice cover of the lake using a Zullig corer. Once taken the core was cut into 5cm blocks and then stored at -18°C. It had been partially melted and refrozen before this study commenced.

3.2.1. Sample Preparation:

As the scales are small in size the sample was concentrated and filtered to remove the majority of the diatoms and any debris that may have been present. To concentrate the sample 0.5 grams dry weight of sediment was mixed in 12 ml of distilled water for 5 minutes or until resuspended using a vibrating mixer (Vor-mix VM80). The top 11ml was filtered through a 0.8µm filter to produce 10 ml of filtrate, which was centrifuged at 2000rpm for an hour. After centrifuging, the top 8ml of supernatant was decanted off leaving a concentrated 2ml sample for the negative staining and shadow casting preparation of TEM grids.

After concentration the sample was fixed onto grids by a 60 second treatment using 4% aqueous osmium tetroxide. Six grids were prepared for each sample, three were negatively stained for 70 seconds in 3% Uranyl acetate. Three grids were shadow cast in $5x\ 10^{-6}$ Tor using chromium metal at a 30° angle for 2 seconds using 50% source in a Dinovar evaporator. The body and cyst scales on the negatively stained grids were counted from 10 fields of view in 10 squares for each of the three replicates at 15 000x on a Hitachi H300 TEM. The shadow cast grids were used in place of damaged grids and for photography.

The filtering of the sediment to remove large sized debris may have produced false zeros in the data by filtering out an undetermined portion of the scales along with the larger debris. But this is not considered important as the filters were washed and pore size was larger than scale size.

3.2.2 Diatom Stratigraphy:

To prepare slides to determine the diatom stratigraphy of Ace Lake the sediment sample was first desalinated to prevent salt crystal formation. A small amount of wet sediment was rinsed with 10ml of distilled water and centrifuged three times, to remove the majority of the saline water. Once rinsed, the sample was shaken and allowed to settle for 3 secs and approximately 1 ml was removed using a Pastuer Pipette and placed on a 22mm x 40mm coverslip. The coverslip was heated at 50°C for an hour or until the sample had evaporated and then mounted with 4 drops of Naphrax fixative and covered with a slide. The completed slide was then left on a warm (25°C) hotplate to facilitate the spreading and setting of the Naphrax. Three replicate slides were made for each sediment sample.

Three hundred diatoms were counted from each of the replicate slides, differentiating them into the six parameter groups. Six reference species were chosen to gauge the changes in the assemblage with salinity. These species were chosen with the hypothesis that the proportion of each group would vary with the salinity changes in the lake.

Two species were chosen to represent a "pioneer marine" environment. The species chosen are halotolerant having broad salinity tolarences which enable them to exist in a wide range of salinities, making them most likely to colonize an area with varying salinity, which is typical of a neritic environment. These representative diatoms were chosen under the guidence of A. McMinn, University of Tasmania. The species were Pinnularia microstauron (freshwater), Stauroneis Sp. A (freshwater), Nitzschia cyclindrus (pioneer marine), Nitzschia curta (pioneer marine), Eucampia antarctica (marine); Thallasiosira, Porosira, Coscinodiscus and Asteromphalus, were counted as Centrics (marine). Other diatoms were noted as such and used to determine the total cells counted. If the slides did not contain three hundred diatoms the average number of diatoms on the three replicate slides was taken as representative of the assemblage at that time.

The sediments of the five lakes used as a comparison study to Ace Lake contained high amounts of fine clastic material, unlike those of Ace Lake

and consequently the sediment samples were filtered before enumeration which may have caused some loss of particles. Errors in the Ace Lake data are considered to be low because the samples were not filtered.

3.3 Results:

3.3.1 Diatom Stratigraphy:

Five main assemblage changes were observed throughout the core, which are similar to the three changes observed by Bird *et al.*, (1991) (Fig. 3.2).

•Unit A; 0-22 cms: Benthic diatoms, mostly freshwater dwelling, dominate the assemblage in the top segment of the core, with Stauroneis being the dominant species (14% total cells). This assemblage also contained the two pioneer species N. curta (1.75% total cells) and N. cylindrus (0.96% total cells) and numerous other brackish species, but no open marine species were present (Figure 3.2).

•Unit B; 22-35.5cms: Fresh water species were present, but the dominant species present are pioneer (26% of total cells) and open marine dwelling forms (6.7% total cells).

•Unit C; 35.5-135 cms: Open marine (4.82% total cells) and pioneer species (40% total cells) were dominant throughout this section of the core. It was the only section of the core that contained Eucampia antarctica (0.54% total cells). Large numbers of the freshwater species Stauroneis sp. were found only in the lowest sample of this unit (30% total cells).

•Unit D; 135-170 cms: This unit was dominanted by the freshwater dwelling species, P.microstauron (86% total cells), however, the pioneer species were present in lower samples of the unit (6.3% total cells).

•Unit E; 170-185 cms: This segment was mixed and had three distinct regions. From 170-175 cms there was a dominance of the pioneer species (26% total cells), with small numbers of open marine species present (1.3% total cells). From 175-180 cms there was a mix of N. cyclindrus; the pioneer species (9% total cells), the centric open marine species (8% total cells) and Stauroneis sp. the freshwater dwelling species (2.5% total cells). From 180-185 cms all species were present in relatively equal proportions, freshwater dwellers (7% total cells), pioneer species (12% total cells) and open marine species (6% total cells), except for the open marine species E. antarctica.

Fig 3.2:

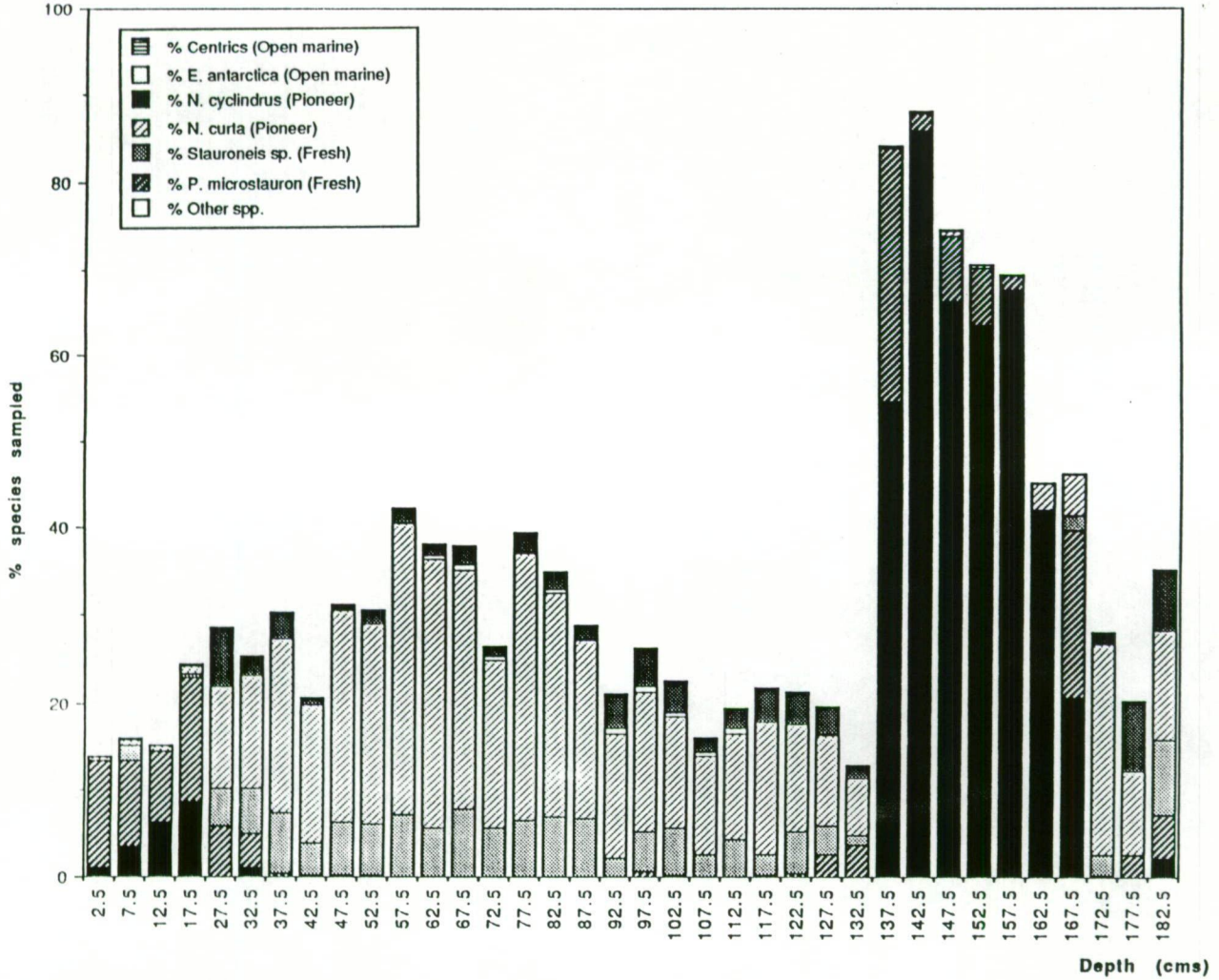


Fig 3.2: Diatom stratigraphy of an Ace Lake sediment core. Abundances of species indicate a marine environment from 25cm-135cm; fresh 135cm-170cm; mixed 170cm-180cm.

3.3.2 Scales:

The P. gelidicola cyst scales always occurred in conjunction with the vegetative body scales in the sediments. At the top and bottom of the sediments they were rarely found and seemed to occur mostly through the region of 75-150cms with maximum cyst scales at 10/field of view (units C-D) (Figure 3.3). Body scales reached a maximum in the top 15cms of sediment (21.8/FOV).

3.4 Discussion:

The six reference species were used to illustrate the change in salinity from freshwater to marine. The species were used singly or were grouped as a particular parameter type such as pioneers, freshwater dwelling or open marine species. The concentrations of these species and parameters in the core samples varied dramatically to show at least one marine and freshwater phase in the lake's history (Fig 3.2). In order to determine the time sequence of these changes further dating was performed on the Ace Lake core. This dating produced ages of 6740 years at 135-140cms and 8380 years at 165-170cms (M. Bird *pers comm.*), suggesting that the sedimentation rate varied throughout the Ace Lake core probably in response to marine and lacustrine developments in the lake's history. Extensive dating by Bird *et al.*, (1991) on a Highway Lake sediment core showed two different sedimentation rates (1.2 mm/yr and 0.6 mm/year). They suggest that these rates represent marine and lacustrine stages of the lake's evolution respectively. Organic Lake showed similar sedimentation rates.

3.4.1 ^{14}C Dating:

In order to be able to determine the broad scale evolution of Ace Lake in real time, the physical data (Fig 3.4), the diatom (Fig 3.5, 3.6) and scale data (Fig 3.7) were graphed according to time using the new dates obtained for this study as well as the dates obtained by Bird *et al.*, (1991).

There are large "reservoir" effects in coastal Antarctica due to the upwelling of deep marine water near the coast. The reservoir effect for the

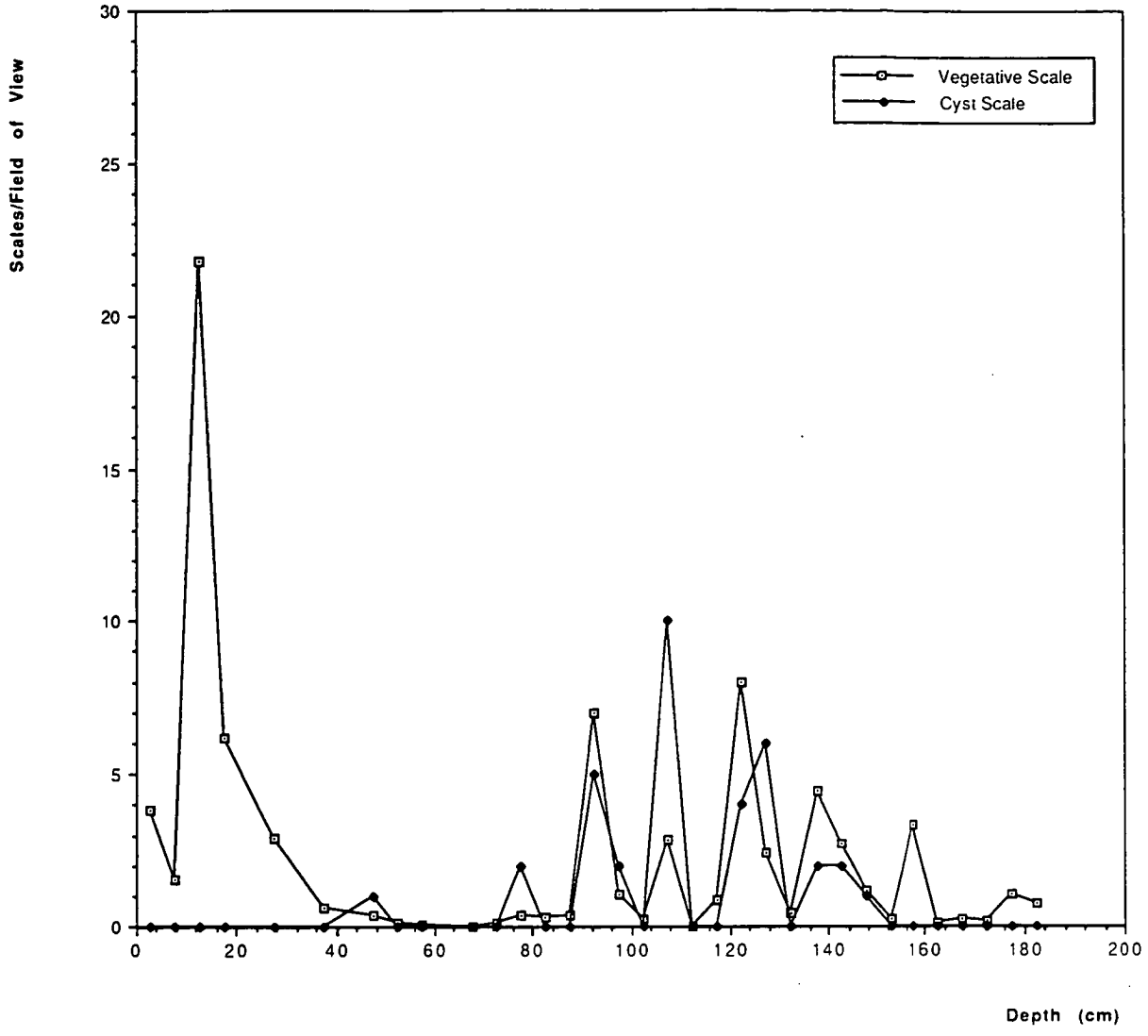


Fig 3.3: P. gelidicola scale concentrations in Ace Lake sediments. Note that cyst scales always occur in conjunction with body scales except in the top 37cms.

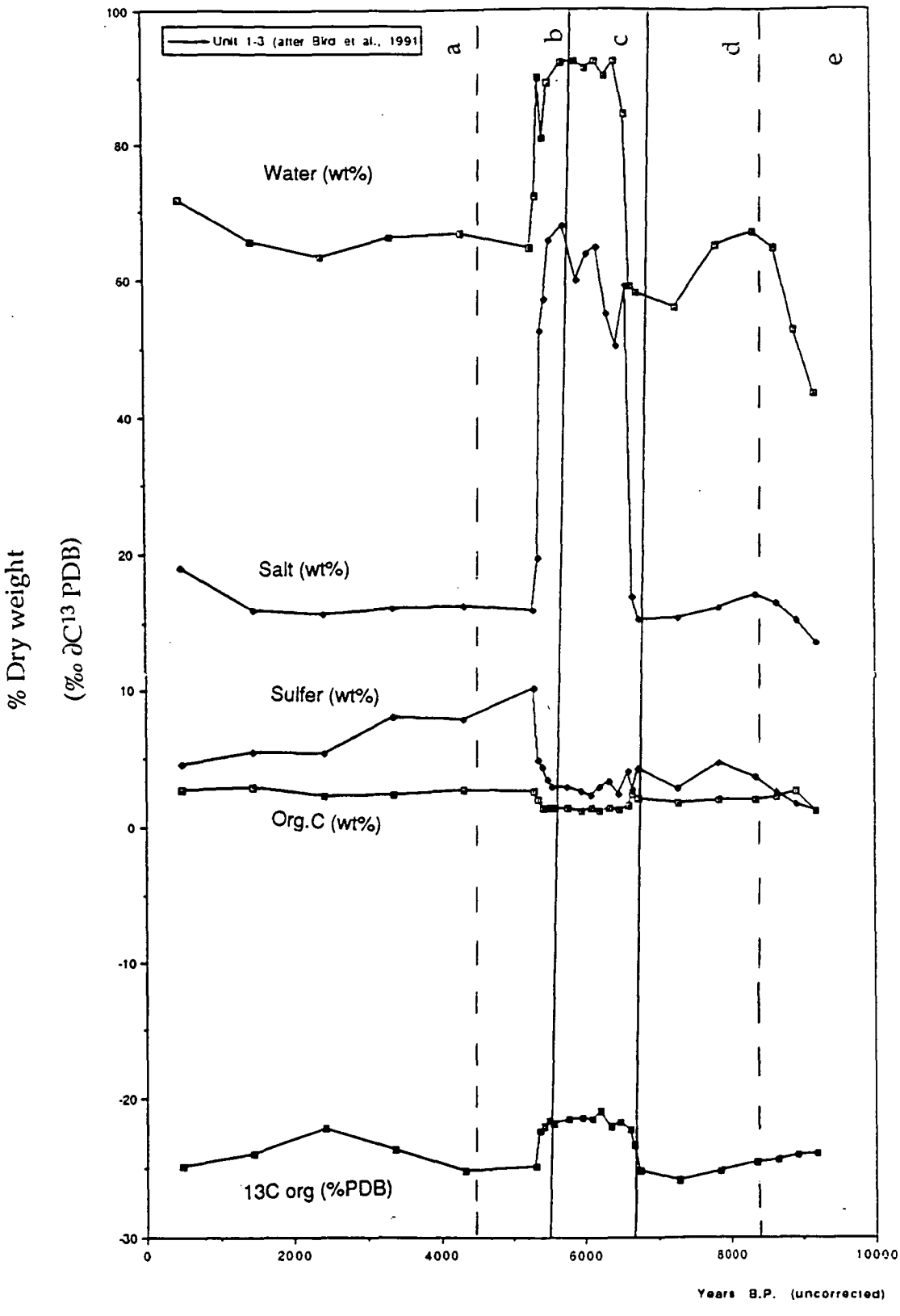


Fig 3.4: Physical parameters of an Ace Lake sediment core plotted vs. uncorrected time (after Bird et al., 1991)

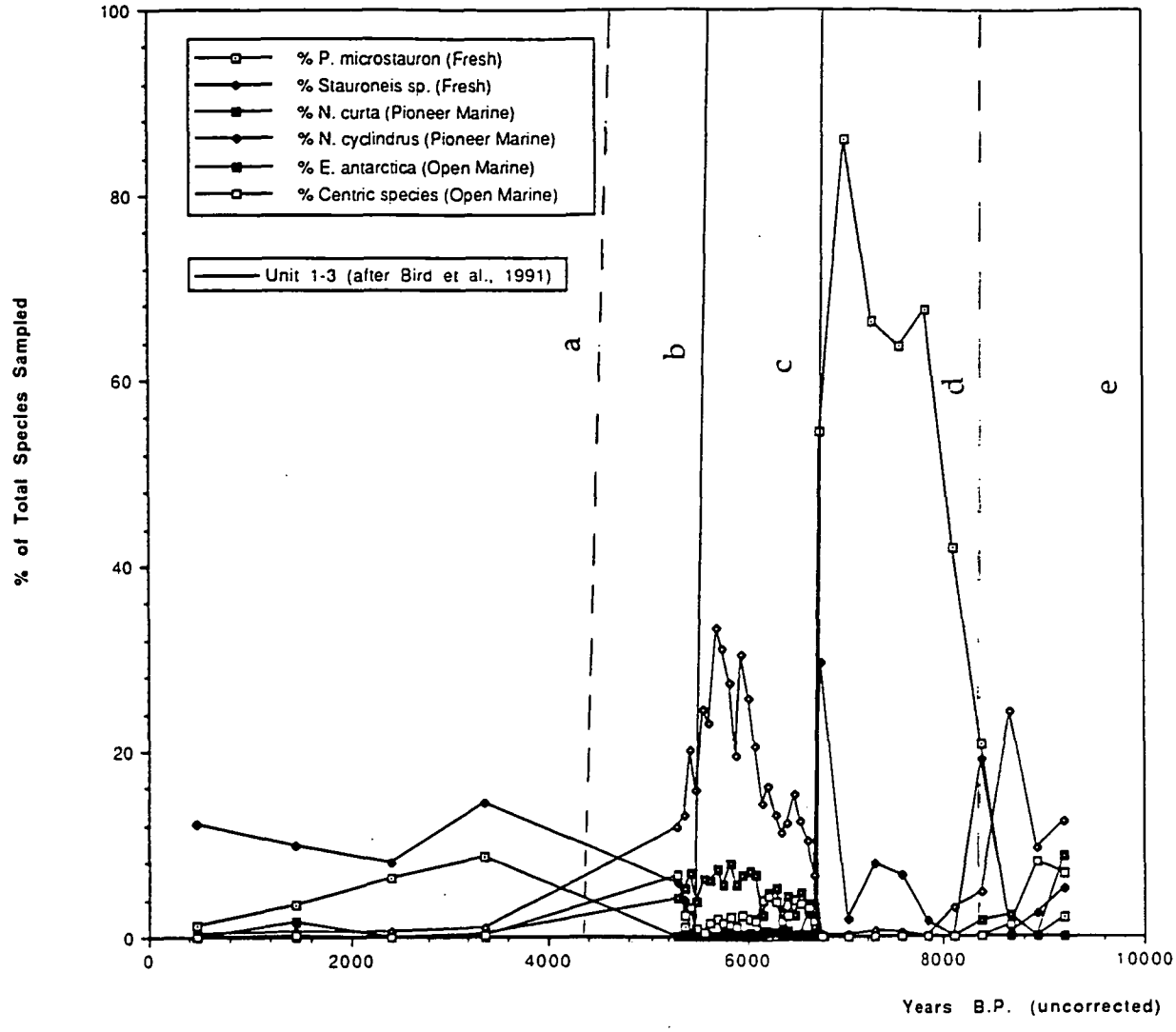


Fig 3.5: Diatom Stratigraphy of an Ace Lake sediment core plotted vs. uncorrected time

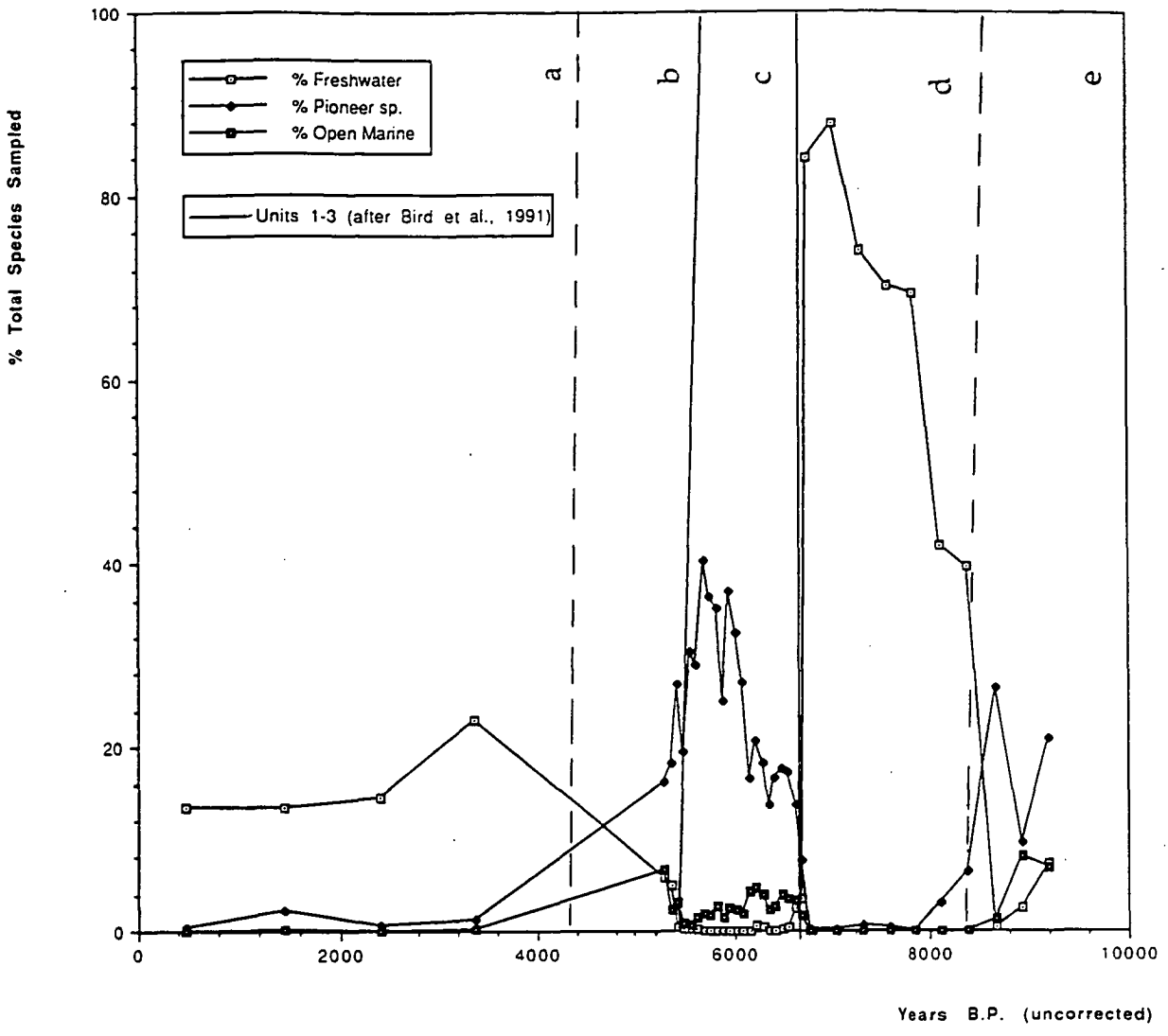


Fig 3.6: Diatom parameters of an Ace Lake sediment core plotted vs. uncorrected time

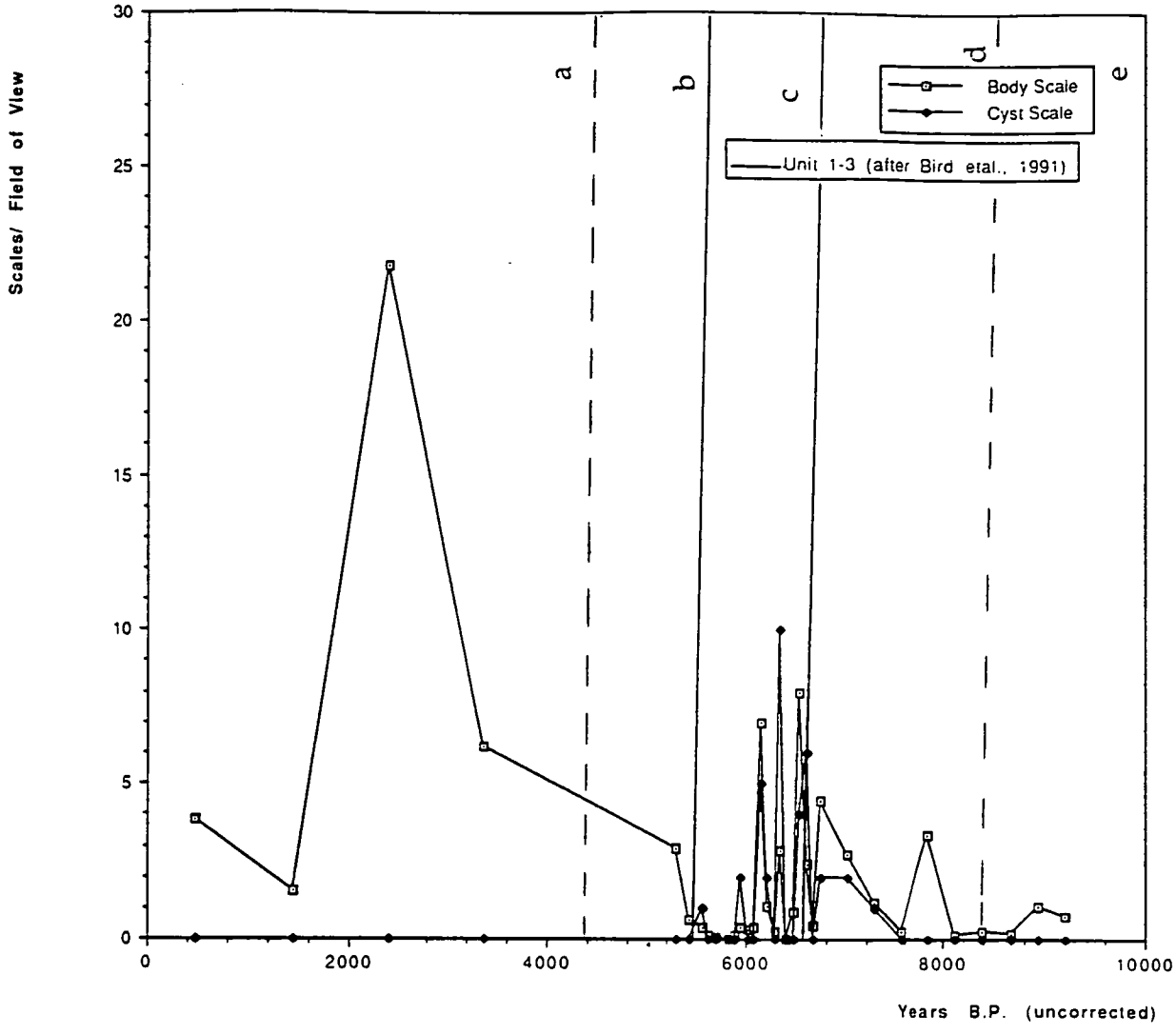


Fig 3.7: P. gelidicola scale concentrations in an Ace Lake sediment core plotted vs. uncorrected time

terrestial environment is zero and for marine areas in the vicinity of Davis base is 1000-1300 years (pers comm. Michael Bird, Australian National University). Linear regression of seven ^{14}C dates in Highway Lake indicate a lacustrine reservior effect at the sediment-water interface of approximately 1000 years; which is similar to that seen in Deep Lake (Bird *et al.*,1991). Based on this the total reservoir effect for sediment deposited under marine conditions in the Vestfold Hills lakes was estimated by Bird *et al.*, (1991) as 2200 years.

In order to assess maximum and minimum sedimentation rates in Ace Lake a reservoir effect of 1000 years for the sediment-water interface in lacustrine conditions was used to adjust dates in the portion of the core that was determined as lacustrine from the presence of freshwater dwelling diatoms. An effect of 2200 years was used as a total reservior effect for sediments under marine conditions. The two different corrections were used in order to obtain the most conservative minimum time estimates for the duration of a marine phase in order to rule out the possibility of a "splashover" rather than a true marine incursion. This adjustment indicated sedimentation rates of approximately 1.4 mm/yr in the marine environment (55cm-137cm) and a sedimentation rate of 0.18 mm/yr in lacustrine conditions (137cm-167cm). This gives a total sedimentation rate of 110 cm in 500 years of marine incursion a longer period than could be expected for a single splash over event. These sedimentation rates compare favourably with those of Highway Lake and Organic Lake (Bird *et al.*, 1991).

With these corrections, however, the corrected date at 35-75 cm is younger (at 3910 years B.P.) than the corrected date at 20-35 cm above it (at 4150 years B.P.). This indicates the reservoir age corrections determined for the Davis Base area today do not strictly apply in the past. It is certain that a reservoir effect must occur in the past, however, because it is not well known, all data has been plotted using uncorrected ages to avoid confusion. The scale results and the diatom stratigraphy showed little correlation, but separately the five units determined from the diatom stratigraphy demonstrated the occurence of five distinct phases in the evolution of the lake (Fig 3.5). This refines somewhat the three phases

suggested by Burton and Barker (1978) and Bird *et al.*, (1991). Unit a and b are similar to the Bird *et al.*,(1991) unit 1, similarly unit c corrosponds to unit 2 and units d and e to unit 3.

3.4.2 Diatom Stratigraphy:

•Unit E (170-185cms; 9200-8380 years B.P):

This unit is the most complicated, and is intrepreted as comprising the sediment of the lake when it was first forming. This segment of the core shows an upcore increase in all of the physiochemical parameters except $\partial^{13}C$. The diatom assemblage is equally mixed throughout with the presence of both fresh and open marine diatoms (Fig. 3.6). A strong melt water influence at that time is indicated by the presence of Pinnularia microstauron, a species which is found primarily in fresh water lakes and melt water streams of the of the Vestfold Hills. The simultaneous presence of the open marine centric species suggests a strong marine influence. Further, the sediments in this portion of the core are not laminated, indicating that circulation was not restricted. Diatom concentrations were low in this section, suggesting that they did not actually grow there but had flowed through water movement. Therefore, the unrestricted marine input and the meltwater input would have effectively brought about the paradoxical situation of both fresh and marine species occuring at one time in the water column. As the lake was more isolated, the mixing influence of the marine and freshwater inputs decreased and the lake became increasingly stratified, developing an anoxic basin, registered by an increase in sulphur levels in the lake supporting a dominant assemblage of pioneer species. The diatom parameters suggest a decrease in the marine influences and a shift towards lacustrine conditions through time with an increase in the pioneer species in the top segments of this unit (Fig 3.6). This is supported by the slight increase in sulphur content and organic carbon. In contrast, the increase in the salt and water content of the core suggest an increasing marine influence (Fig 3.4).

The marine species of phytoplankton found in a majority of the inland lakes in the Vestfold Hills are often dispersed by the sea spray (M. Bird pers. comm). To determine if the marine input was direct rather than spray, a study of 5 other lakes, from the Vestfold Hills region was carried

out; Medusa, Scale, Cat, Collerson, and Lake C. These lakes are inland and have never been flooded by a marine incursion. The basal sediments of these lakes were examined in order to determine the marine diatom composition and abundance in purely freshwater lakes, for comparison with Ace Lake (Fig 3.8).

The sediments of all five lakes contained only fragmented diatom frustules in low numbers. Centrics were the most dominant diatom group sampled. The results suggest that the input of marine diatoms by sea spray produces mostly diatom fragments in low densities. The presence of whole marine diatoms in Ace Lake indicates a direct marine influence.

An alternate interpretation is that the lake may have been fresh when it was first formed and the marine and pioneer species present in the sediments may have been introduced to the lake by animal vectors, such as penguins. Studies carried out on freshwater Squa lake on Horseshoe island, by Wasell and Hakansson (1992), indicated that the input of marine diatom species, both pioneer and centric, by animal vectors was associated with an increase in organic carbon in the lake. Rookery lake on the end of Long Peninsula also has a high organic input from the rookeries situated around it. The organic content of the Ace Lake core is almost continuously low throughout the core and therefore it is unlikely that there was any association with animal vectors (Fig. 3.4). Ace Lake is also further from the coastal regions than either of the above lakes (Fig 1.1) and therefore was less likely to have been visited regularly by seals or penguins.

Whole diatom specimens were present in the unlaminated basal sediments of the Ace Lake core and it had low organic content. This suggests that the lake was probably a high energy inlet on an open marine coastline when first forming. It was influenced by two major water inputs, marine and freshwater, which were responsible for the mixing of the sediments and the presence of both open marine and freshwater species at one time

Unit D (135-170cms; 8380-6674 years B.P):
Throughout this period the lake increased in organic content and maintained it's anoxic basin as seen by the sulphur levels of the core (Fig

Fig 3.8:	Lakes					
Species	Scale	Collerson	Lake C	Medusa	Cat	Ace
Freshwater	2	0.3	5	1	3	3
Pioneer	3	6	1	3	1.3	18.3
Open Marine	6	8	3	7	6	5.3
Total Cells	11	14.3	9	11	10.3	26.6

Fig 3.8: Fragments (greater than half frustules) of the parameter species found in filtered samples of sediment cores from 5 lakes of the Vestfold Hills. Values represent number of fragments per slide that were greater than half original frustule size: except for Ace Lake values where whole frustules were sampled as well as fragments.

3.4), which are similar to Ellis Fjord levels (Bird *et al.*, 1991). The dominant species in the sediment was Pinnularia microstauron, with varying numbers of Stauroneis sp. and only a small number of pioneers present in the lower sediments which reduce in number up-core (Fig. 3.5). This data suggests that the lake became fresher during this period. It appears that as the melt water input into the lake increased with ice cap retreat, the lake became flushed, causing the marine species to fall out of the system. As Ace Lake is only 2m below it's sill at the present time, it is probable that the initial marine influence was not long lasting, and only minor isostatic uplift was needed to isolate the lake. The flushing of the lake was evident in the sulphur isotope results of Burton and Barker (1978).

Watts Lake is believed to have undergone similar flushing to Ace Lake 2000 years ago (Pickard *et al.*, 1986), causing a similar change in assemblage from brackish pioneers to freshwater species as the lake formed a permanent freshwater lens. Bronge (1989) determined that Watts Lake became fresh over a period of 300 years, due to the stratification and upper mixing of the lake, with only a moderate melt-water input (2 m^3/s for 2 summer months). His figure is much shorter than the 2000 years suggested by Pickard *et al* . (1986). Even taking into account the possible reserviour corrections of the dates of 1150 years, it is possible to determine that Ace Lake became purely freshwater over a minimum of 1700-2500 years. This compares favourably to the time Bronge (1989) proposed for Watts Lake, a lake which is situated next to a large drainage system (Druzby). Ace Lake is not situated near a similar system and therefore it would be expected that freshwater input would have been less than that experienced by Watts Lake.

•Unit C (37.5-135cms; 6674-5430 years B.P):
The diatom assemblage changed dramatically through this section with P. microstauron, disappearing in favour of both the pioneer species (N. curta and N. cyclindrus) and marine species (the centrics and E. antarctica) (Fig 3.5). Increased species diversity is indicated by the high number of "other species" and the lower number of pioneer species; Nitzschia sp. (Fig 3.6). This was the only section of the core where Eucampia antarctica was sampled (Fig 3.5). Therefore it it is interpreted as the only "open" marine

section of the core, as Eucampia antarctica is a open marine species, not associated with sea ice or fast ice (Stockwell *et al.*, 1991).

The constant $\partial^{13}C$, sulphur and organic carbon trends of unit C (Fig 3.1), suggest a marine environment. However, the $\partial^{13}C$ values of the Ace Lake core are much lower than the recorded levels in the Ellis Fjord and also of the Organic Lake and Taynaya Bay (Bird *et al* ., 1991). Because these sediments in Ace Lake were banded it is possible that the marine influence was restricted (similar to Ellis Fjord) but the lower $\partial^{13}C$ values indicates that the system was not as productive. It is possible that the connection to the marine source was tidal. The presence of intermixed diatom and sandy varves in the sediments are indicative of a tidal input (Bronge, 1989). However, grain size analysis and x-ray examination of the Ace Lake core was not carried out before it was thawed, so the presence or absence of intermixed varves could not be determined. The $\partial^{13}C$ values of the core rise slightly at 6216 years B. P. (95 cms; Fig 3.1), which may indicate the transition of the lake from a marine environment to a marine inlet. This change is also evident in the diatom stratigraphy, as a distinct increase in the concentration of the pioneer species and a decrease in the open marine species (Fig 3.6). This change is similar to the results of Wasell and Hakansson (1992), who found that Squa lake, on Horseshoe Island, Antarctica, had three distinct zones of diatoms: marine, brackish and fresh. The brackish zone was signified by an increase in Nitzschia species in particular, N. curta and N. cylindrus,which show a preference for shallower regions. There was however no increase in the sulfur, organic carbon content of the core nor in the $\partial^{13}C$ values at this level and so no evidence of a prolonged marine connection (Fig 3.4). These physical parameters increased at 5430 years BP. (35-40 cms; Fig 3.1), and are taken to indicate the definite separation of the lake from it's marine source. This is also shown in the diatom stratigraphy, as E. antarctica was not sampled after 5430 years (Fig 3.5). It is unclear whether this was through sea level decrease or isostatic uplift.

These diatom and physical changes in this segment of the core are interpreted as a marine incursion to the lake, which took place over a minimum of 1200 years. A marine incursion would have disturbed the

meromixis of the lake and made it oxic, but the sulphur levels in the core are equilivent of those of Ellis Fjord (Bird *et al* ., 1991), and therefore it is suggested that there could have been deep annoxic pockets, similar to those seen in Ellis Fjord today. The sediments were still slightly laminated, indicating that the incursion was restricted, perhaps entering from a protected fjord or as a seasonal connection, until the lake was permanently isolated about 5430 years ago.

•Unit B (20-37.5cms; 5430-4336 years B.P):
During the 1000 years approximately that these sediments were laid down, the organic carbon and sulphur in the core increased and the water and salt content dramatically decreased, suggesting that the lake became more stabilised, fresh and anoxic (Fig 3.4). The diatom species in the core reflect this change, with an increase in the freshwater species and a decrease in the pioneer species up core (Fig 3.6). This suggests the formation of a fresher water lens at the surface of the lake and the stratification of the water column. A similar change from marine to freshwater flora was also observed in Squa Lake (Wasell and Hakansson, 1992). As the salinity of the surface waters of Ace Lake today are about 14 ‰ (Burch, 1988), it is suggested that the melt water input into the lake has decreased with time, and flushing decreased or ceased completely even though the lake level is only 2 m below sill height (M. Bird, *pers comm.*). If this is correct it suggests the precipitation of the region may have decreased during the past 8000 years contrary to Pickard *et al.*, (1986). Alternately, the drainage pattern of the region may have altered channeling less meltwater to the lakes drainage basin and reducing the freshwater flowing into Ace Lake.

•Unit A (0-20cms; 4336-481 years B. P.):
Ace Lake appears to have stabilised about 4336 years ago. There was an increase in the freshwater species in the lake and the marine species disappeared, with only low numbers of pioneer species present (Fig 3.6). These pioneer species have been suggested to be associated with the benthic mats of the lake (J. Gibson *pers. comm.*), but this has not been studied. The high concentration of the freshwater species, Stauroneis sp (Fig 3.5), could be indicative of it's establishment as part of the lake's phytoplankton assemblage and not just as a meltwater immigrant like P.

microstauron. This would confirm the formation of the fresher water lens at the surface of the lake. This indicates increased input of meltwater into the lake or decreased evaporation producing a fresher surface lens. The overall diatom straigraphy suggests that the lake reached an equilibrium during this period. At 4336 years ago, P. microstauron was 8% of the total cell number, with this percentage decreasing to 1% 400 years ago, indicating a decrease in meltwater input into the lake. There was an increase in the water level of the lake of 1m in the period of 1978 - 1982 (Pickard, 1983) and of 24 cms from 1985 to 1989 (J. van den Hoff *pers. comm.*). These recent water level changes may be indicative of the long term trend of decreasing meltwater input.

3.4.3 Scales:

P. gelidicola has been a member of the phytoplankton community of Ace Lake since it was first formed. Cyst scales first appeared at 147cms in the core (Fig 3.3) or at least 7200 years ago (Fig. 3.7). Both cyst and body scales show a positive correlation with the increase in fresh water diatoms at this depth. During the marine incursion the cells and cysts maintained their presence decreasing as the open marine species disappeared (Fig 3.6, 3.7). As the lake became fresher the vegetative cells increased in number to reach a maximum during conditions that were similar to todays. No cysts were present above 47cms. The species is more abundant in what are interpreted as meromictic conditions in unit A and B, where fresher waters are present. These results are concommitant with those of van den Hoff *et al.*, (1989), who found that peak Pyramimonas gelidicola vegetative cells occured in the top segment of an Ace Lake sediment core. There were however some discrepancies in the two results in that the abundence of cyst scales in the earlier study occurred during periods with low vegetative scale representation, except in the top 10 cms of the core. In this study no cyst scales occurred above 47 cms of sediment and when they were present they occurred concurrently and proportionally with the body scales (Fig. 3.3).

The results of neither study support a conclusion that the cells produce cysts only during poor conditions, which is supported by the rigorous culture experiments of Chapter Two. The pattern of Pyramimonas

gelidiocla scales in this case suggest two alternative hypothesises: 1.) Changes in Pyramimonas gelidicola populations are sensitive to other parameters than the physical changes in the lake, or 2.) The cysts are produced annually as an overwintering device. It must be noted however the nonoccurrances of P. gelidicola scales could be artifacts of the filtering process that removed the larger diatoms and so some trends could be disguised.

To see how well the diatom stratigraphy in Ace Lake reflected regional climate changes, the sea surface temperature of the Southern Ocean over the past 10 000 years (Pichon *et al.*, 1992) and the diatom and scale trends in the Ace Lake sediment core were compared. These showed no significant correlations (Fig. 3.9). Sea surface temperature and climate change are well correlated with the changes in diatom assemblages in open ocean sediments (Leventer and Dunbar, 1988, Stockwell *et al.*, 1991, Pichon *et al.*, 1992). The only changes indicated by the diatom assemblage in Ace lakes sediments were local ones such as meltwater flushing and marine incursions or isolation. These dramatic localised events mask any climate changes that may have occurred. This effect is also reported by Wasell and Hakansson (1992), in their study of Squa lake, Horseshoe Island.

3.5 Conclusions:

A study of diatom assemblages, combined with results of physical parameters (Bird *et al.*, 1991) indicate that Ace Lake was first isolated from the ice cap more than 8100-9200 years ago. This date differs from the 6000-8000 years suggested by Pickard *et al.*, (1986). Ace Lake was subject to two main influences during its formation. A melt water input from the retreating ice cap and a marine influence from the open ocean. These competing influences are evident in the diatom stratigraphy and unlaminated sediment of unit E. The mixing capability of the marine influence decreased as isostatic uplift occurred isolating the lake. As the marine influence decreased, freshwater input flushed the lake over the course of approximately 2000 years (~8600-6600 years B.P.) and the lake became stable and meromictic (unit D). Sea level maxima in this area is estimated to have occurred 5-6000 years ago (M. Bird *pers. comm.*), suggesting that seawater could have flooded over the 2 metre sill into Ace

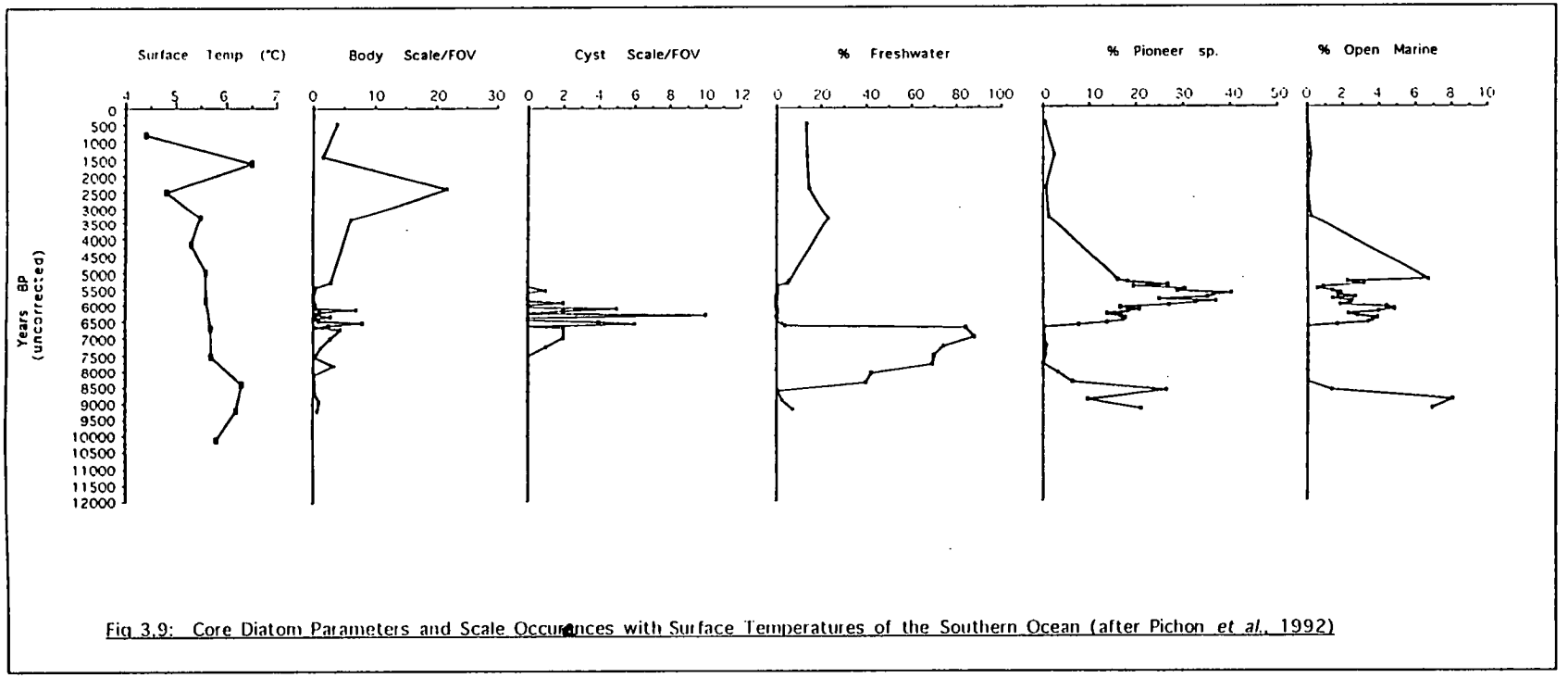


Fig 3.9: Core Diatom Parameters and Scale Occurrences with Surface Temperatures of the Southern Ocean (after Pichon *et al.*, 1992)

Lake and disturbed the freshwater meromixis. The lake was marine for approximately 1200 years, from 6600- 5400 years BP (unit C). The sediments laid down in this period were laminated and sulphur was present indicating the marine input was restricted. $\partial^{13}C$ data indicates that production in the lake at this stage was at its peak, but less than that found in Ellis Fjord and other lakes of the region at that time (eg. Organic lake: Bird *et al.*, 1991). Sea level decrease and/or isostatic uplift caused the re-isolation of the lake at approximately 4800-5400 years ago which was followed by about 1000 years of slow flushing to a stable meromictic basin, with the lake developing a fresher surface layer through melt water input (unit B). The diatom and physical parameter data indicate that the lake has been stable and meromictic for approximately the past 4000 years (unit A). Increases in the lake water level that have been measured since 1978 (Pickard, 1983, J. van den Hoff *pers. comm.*), indictate at least two changes in the short term climatic history of the region, as the lake could not have increased 1m every four years for the past 4000 years. The decrease in the P. microstauron data seen in unit A over approximately 3500 years could be indicative of a decreasing meltwater input as the species is introduced into the lake by meltwater streams. However, such water level changes in the lake are too short term to be reflected in the diatom stratigraphy. The main climatic changes that would have affected the lake were the warming of the climate and the consequent increase in precipitation and sea level.

No correlation with sea surface temperature was found in either the diatom or the scale data. The lack of trends in the P. gelidicola scale data alone could also indicate that the meromictic lake systems are too stable for their phytoplankton assemblages including P. gelidicola to be affected by climate changes such as regional temperature variations.

The results of this study indicate that palaeoclimatic research is better served in the open ocean, where biological and physical parameters are more sensitive to regional climate changes.

Chapter 4:

Summary of Research:

4.1: Summary

Pyramimonas gelidicola has a broad distribution across the Vestfold Hills and the cyst and body scales of this species have been found in the sediment of the lakes and marine areas of the region. This suggested that P. gelidicola had the potential for being a climatic indicator. This study was conducted to determine the possibility of using P. gelidicola as a palaeoclimatic tool. Growth experiments were performed on two strains of P.gelidicola to determine the conditions under which the species survives, thrives and encysts. These results were then used in conjunction with the scale concentrations and diatom stratigraphy of an Ace Lake sediment core to determine the evolution of Ace Lake in the Vestfold Hills.

The results of the culture study showed that P. gelidicola was a very versatile organism, with a broad range of tolerances and optimas. The Ace Lake strain of the alga grew better than the Prydz Bay strain in all conditions, producing more cysts and higher cell numbers. The alga grew in a broad range of salinities from 5 to 80‰, temperatures from -1.5-18°C,

nutrient media conditions of $F/_{50}$ to 2F and light levels of 3 to 20 $\mu Em^{-2}s^{-1}$. Optimal growth of the Ace Lake strain occurred at 6-8°C, 35-60 S‰, $F/_2$-F media and 10 $\mu Em^{-2}s^{-1}$. The Prydz Bay strain grew optimally at 60 S‰, in F-2F media at 10-20 $\mu Em^{-2}s^{-1}$, but showed little response to temperature changes. Cyst production was maximised in good nutrient conditions in both strains and the Ace Lake strain showed increased production in hypersaline (60‰) conditions. Temperature had a random effect on cyst production and cysts were produced throughout the experiments irrespective of growth phase.

By examining the distribution of six diatom species as indicators for specific conditions and the cysts of Pyramimonas gelidicola, the evolution of Ace Lake was hypothesised. These diatom species were Pinnularia microstauron (Freshwater), Stauroneis sp. (Fresh to brackish water), Nitzschia curta (Pioneer marine), Nitzschia cyclindrus (Pioneer marine), Eucampia antarctica (Open marine) and the marine Centric species including Thalassiosira, Porosira, Coscinodiscus and Asteromphalus (open marine). The use of P. gelidicola as a climate indicator is limited because of the wide range of tolerances that the species has and also the production of the cysts in connection with good nutrient conditions and hypersalinity (>60‰). No trend was found in the scale data to match the diatom responses to the freshwater flushing or the marine incursion therefore, the scales are probably not influenced by localised events because of the broad tolerances of the species. Therefore, the proposed lake evolution is based on the changes in distribution of the parameter species in the sediment core.

The variation in concentration of these species in the sediment enabled the construction of an evolutionary history for Ace lake. The lake has evolved over the past 8000-9000 years through 4 different physio-chemical modes. The lake when first formed was influenced by both open marine waters and a meltwater input (9200-8100years B.P.). Isostatic uplift adjusted the altitude of the lake basin and it became purely fresh through flushing of the lake by meltwater. This process occurred over the course of about 2500 years (9200 to 6700 years B.P.). About 6100-6300 years ago global sealevel rose due to deglaciation and the lake was subject to a marine incursion.

Ace Lake was marine influenced for 1200 years although the basin must have been restricted, allowing for the lamination of the sediments. Isostatic uplift re-isolated the lake at 4800-5400 years B.P. and it began to freshen at the surface due to meltwater input and to stabilise to a meromictic condition over the course of 1000 years. The lake appears to have been stable for the past 3000-4000 years. The relatively fresh surface layer of Ace Lake is maintained by the seasonal melt water that it receives through ice and snow melt.

Cyst and vegetative scales of P. gelidicola occur through out the sediment core with the majority of the body scales occurring in the last 3000-4000 years, but no cyst scales were present during this time. Comparisons of the changes in the sea surface temperature of the Southern Ocean over the past 10 000 years with the scale and diatom data of the core showed no correlations. This indicates that lake environments cannot be used as an indicator of the climate changes that affect the ocean surface temperature. This is most likely due to the effect of local or regional changes such as marine incursions and freshwater flushing that mask any record of climatic changes that may have occurred. Therefore, studies of climate changes in the lakes of the Vestfold Hills would not be as indicative of climate change as a similar study conducted in the marine regions.

Future studies involving P. gelidicola should include an *insitu* study of cyst concentration in the water column, lipid storage of P. gelidicola vegetative cells and measurements of changes in cell volume, which would aid in determining the survival mechanism of the alga through the Antarctic winters. Further study is also needed to determine if salinity has an effect on the cyst production of P. gelidicola and day/night regimes and high intensity light should be studied to determine if cyst production is a function of day length or high light intensity.

Regular measurements of lake surface levels may indicate any increases or decreases in ablation, precipitation or evaporation that may affect the Vestfold Hills region and therefore, give an indication of regional climate changes. Dating of other lakes on Long Peninsula and examination of their basal sediments could help in determining the formation of the lake and

the evolution of the Vestfold Hills in comparison with other oases of the Antarctic continent.

Bibliography:

Adamson, D. A. and Pickard, J., 1983. Late Quarternary ice movement across the Vestfold Hills, Antarctica. In: R. L. Oliver, P. R. James and J. B. Jage (Editors), *Antarctic Earth Science.* Aust. Acad. Sci., Canberra, pp. 465-469.

Adamson, D. A. and Pickard, J., 1986a. Physiography and geomorphology of the Vestfold Hills. In: J. Pickard (Editor), *Antarctic Oasis.* Academic Press, Sydney, pp. 99-139.

Adamson, D. A. and Pickard, J., 1986b. Cainozoic history of the Vestfold Hills. In: J. Pickard (Editor), *Antarctic Oasis.* Academic Press, Sydney, pp. 63-97.

Aken. M. E. and Pienaar, R. N., 1981. Observations on the Reproduction of Pyramimonas parkeae Norris et Pearson (Prasinophyaceae). *S Afri J. Sci* 77: 324.

Allison, I., 1989. Antarctic Sea Ice in the Weather and Climate System. ASAC Conference and Workshop on Antarctic Weather and Climate, Adelaide, July, 1989. *Extended Abstracts*, pp. 75-85.

Bayly, I.A.E., and H.R. Burton, 1987. Vertical distribution of *Paralabidocera antarctica* (Copepoda: Calanoida) in Ace Lake, Antarctica, in Summer. *Aust J Mar Fw Res* **38**, 537-543.

Belcher.J. H., 1968. A study of Pyramimonas reticulata Korshikov (Prasinophyceae) in Culture. *Nova Hedwigia*, **15**: 179-190.

Belcher. J. H., 1969. Further observations on the type species of Pyramimonas (P. tetrarhynchus Schmarda) (Prasinophyceae): an examination by light microscopy, together with notes on it's taxonomy. *Bot. J. Linn. Soc.*, 62: 241-253.

Belcher. J. H., 1970. The resistance to desiccation and heat of the asexual cysts of some freshwater Prasinophyceae. *Br. Phycol. J.*, **5**: 173-177.

Bird, M. I., Chivas, A. R., Radnell, C. J. and Burton, H. R., 1991. Sedimentological and Stable-isotope Evolution of Lakes in the Vestfold Hills, Antarctica. *Palaeogeogr. Palaeoclimotol, Palaeoecol.* **84**: 109-130.

Bronge, C., 1989. Holocene Climate Fluctuations recorded from lake sediments in Nicholson Lake, Vestfold Hills, Antarctica. University of Stockholm, pg. 1-21.

Buck, K. R., Bolt, P. A., Bentham, W. N. and Garrison, D. L., 1992. A Dinoflagellate cyst from Antarctic sea ice. *J. Phycol.*, 28: 15-18.

Bunt, J. S., 1963. Diatoms of Antarctic Sea-ice as Agents of Primary Production. *Nature* , **199**: 1255-1257.

Bunt, J. S., 1964. Primary Production of the undersea ice in Antarctic waters. 2. Influence of light and other factors on photosynthetic activities of Antarctic marine microalgae. *Ant. Res. Ser..*, **1**: 27-31

Bunt, J. S., 1968. Some charateristics of microalgae isolated from Antarctic sea ice. *Ant. Res. Ser.*, **11**: 1-4.

Bunt, J. S. and Lee, C. C., 1970. Seasonal production in Antarctic sea ice at McMurdo Sound in 1967. *J. Mar. Res.* , **28**: 304-320.

Burch, M. D., 1988. Annual cycle of phytoplankton in Ace Lake, an ice covered, saline meromictic lake. *Hydrobiologia*, 165: 59-76.

Burch, M. D. and Marchant, H. J., 1983. Motility and Microtubule Stability of Antarctic Algae at Sub-Zero Temperatures. *Protoplasma,* **115**: 240-242.

Burckle, L. H. and Cooke, D. W., 1983. Late Pleistocene Eucampia antarctica abundance stratigraphy in the Atlantic sector of the Southern Ocean. *Micropaleontology*, **29**: 6-10.

Burton, H. R., 1981. Chemistry, Physics and evolution of Antarctic saline Lakes: a Review. *Hydrobiologia*, **82**: 339-362.

Burton, H. R. and Barker, R. J., 1978. Sulfur Chemistry and Microbiological Fractionation of Sulfur Isotopes in a Saline Antarctic Lake. *Geomicrobiology J.*, **1**: 329-340.

Burton, H.R. and Campbell, P. J., 1980. The Climate of the VestfoldHills, with a note on its effect on the Hydrology of Hypersaline Deep Lake. *ANARE Scientific Reports*, no. **129**. Antarctic Division Kingston Tasmania

Calder, J. A. and Parker, P. L., 1973. Geochemical implications of induced changes in C^{13} fractionation in blue green algae. *Geochim. Cosmochim. Acta*, **37**: 133-140.

Cota, G. F., 1985. Photoadaption of high Arctic ice algae. *Nature*, **315**: 219-222.

Cota, G. F., Prinsenberg, S. J., Bennett, E. B., Loder, J. W., Lewis, M. R., Anning, J. L. Watson, N. H. F. and Harris, L. R., 1987. Nutrient fluxes during extended blooms of Arctic ice algae. *J. Geophys. Res.*,**92**: 1951-1962.

Cota, G. F. and C. W. Sullivan, 1990. Photoadaption, growth and production of bottom ice algae in the Antarctic. *J. Phycol.*, **26**: 300-411.

Davies, A. G., 1990. Taking a cool look at Iron. *Nature*, **345**: 114-115.

Doucette, G. J., Cembella, A. D., and Boyer, G. L., 1989. Cyst formation in the red tide dinoflagellate Alexandrium tamarense (Dinophyceae): effects of iron stress. *J. Phycol.*, **25**: 721-731.

Eslake, D. , Kirkwood, R. , Burton, H. R. and Wang Zipan, 1991. Temporal changes in zooplankton composition in a hypersaline Antarctic lake subject to periodic seawater incursions. *Hydrobiologia*, **210**: 93-99.

Everitt, D. A. and Thomas, D. P., 1986. Observations of seasonal changes in diatoms at inshore localities near Davis Station, East Antarctica. *Hydrobiologia*, **139**: 3-12.

Fiala, M. and Oriol, L., 1990. Light-Temperature Interactions on the Growth of Antarctic Diatoms. *Polar Biology* , **10**: 629-636.

Fryxell, G. A. 1989. Marine Phytoplankton at the Weddell Sea Ice Edge: Seasonal Changes at the Specific Level. *Polar Biology*, **10**: 1-18.

Fryxell, G. A., 1991. Comparison of winter and summer growth stages of the Eucampia antarctica from the Kerguelen Plateau and south of the Antarctic convergence zone. In: Barron, J. and Larson, B., (Editors), *Proc. O. D. P. Sci. Res.*, **119**: 675-681.

Fryxell, G. A. and Prasad, A. K. S. K., 1990. Eucampia antarctica var. recta (Margin) stat. nov. (Biddulphiaceae, Bacillariophyceae): life stages at the Weddell Sea ice edge. *Phycologia*, **29**: 27-38.

Fulford, S. 1990. Phytoplankton of the Vestfold Hills, Antarctica. Honours Thesis, University of Tasmania.

Gallagher, J. B., Burton, H. R. and Calf, G. E., 1989. Meromixis in an Antarctic Fjord: a Precursor to Meromictic Lakes on an Isostatically Rising Coastline. *Hydrobiologia*, **172**: 235-254.

Gardiner, W. E. and Hargraves, P. E., 1979. Pyramimonas amylifera Conrad (Prasinophyaceae): seasonal dynamics of a wild population, and the effects of temperature and salinity on growth and survival in culture. *J. Plankton Res.* 1: 291-300.

Gosselin, M., Lengendre, L., Therriault J-C., and Demers, S., 1990. Light and nutrient limitation of sea ice microalgae (Hudsen Bay). *J. Phycol.*, **26**: 220-232.

Grant, W. S. and Horner, R. A., 1976. Growth responses to salinity variation in four arctic ice diatoms. *J. Phycol.*, **12**: 180-185.

Guillard, R. R. L. and Ryther, J. H., 1962. Studies of marine planktonic diatoms. 1. Cyclotella nana Hustedt and Detonula confervacea (Cleve) Gran. *Can. J. Microbiol*, **8**: 229-239.

Guillard, R. R. L., 1978. Counting Slides. In: Sournier, A (Editor), *Phytoplankton manual*, UNESCO,. 182pp

Hand, R. M. and Burton, H. R., 1981. Microbial ecology of an Antarctic saline meromictic lake. *Hydrobiologia*, 82: 363-374.

Hargraves, P. E. and French, F. W., 1983. Diatom resting spores: significance and stratergies. In: Fryxell G. A. (Editor), *Survival stratergies of Algae*, Cambridge University Press, pp. 49-68.

Hargraves, P. E. and Gardiner, W. E., 1980. The Life History of Pyramimonas amylifera Conrad (Prasinophyceae). *J. Plankton Res.*, 2: 99-108.

Hawes, I. 1990. The effects of light and temperature on photosynthate partitioning in Antarctic freshwater phytoplankton. *J. Plankton Res.*, 12 (3): 513-518.

Heath, C. W., 1988. Annual primary productivity of an Antarctic continental lake: phytoplankton and benthic algal mat production stratergies. *Hydrobiologia*, 165: 77-89

Heywood, R. B., 1977. Antarctic Freshwater ecosystems: review and synthesis. In G. A. Llano (Editor), *Adaptions within Antarctic Ecosystems.* Smithsonian Institute, Wash. D.C., pp. 801-828.

Holm -Hansen, O., El-Sayed, S. Z., Franceschini, G. A. and Cuhel, R. L., 1977. Primary production and the factors controlling phytoplankton growth in the Southern Ocean. In: G. A. Llano (Editor), *Adaptions within Antarctic Ecosystems.* Smithsonian Institute, Wash. D.C., pp. 11-50.

James, P. R. and Tingey, R. J., 1983. The Precambian geological evolution of the East Antarctic metamorphic shield-A review. In: R. L. Oliver, P. R. James and J. B. Jage (Editors), *Antarctic Earth Science,* Aust. Acad. Sci., Canberra, pp: 5-10.
Johnsen, G, and E. Nøst Hegseth, 1991. Photoadaption of seaice microalgae in the Barents Sea. *Polar Biology*, 11:179-184.

Kirst, G. O., 1990. Salinity tolerance of eukaryotic marine algae. *Annu. Review Plant Physiology, Plant Mol. biol.*, 41: 21-53

Korschikov, O. A., 1938. Viznachnik Prisnovodnikh Vodorostei U.R.S.R. IV. *Volocineae,*. Kiev. pp: 184

Kottmeier, S. T., Muscat, A. M., Craft, L. L., Kastendiek, J. E. and Sullivan, C. W., 1984. Ecology of sea ice microbial communities in McMurdo Sound, Antarctica, in 1983. *Antarct. J. US.*, 19: 129-131.

Kozlova, O. G., 1966. *Diatoms of the Indian and Pacific Sectors of the Antarctic*: Washington D. C. (N. S. F.) (Translated from Russian).

Lee, R.E. 1980. *Phycology.* Cambridge University Press, Sydney.

Leventer, A. and Dunbar, R. B., 1988. Recent diatom record of McMurdo Sound, Antarctica: Implications for history of sea ice extent. *Paleoceanography*, 3: 254-274.

Li, W. K. W., Glover, H. E. and Morris, I., 1980. Physiology of carbon photoassimilation by Oscillatoria thiebautii in the Caribbean Sea. *Limnol. Oceanogr.*, 25: 447-456.

Lizotte, M. P. and Sullivan, C. W., 1991. Rates of photoadaption in sea ice diatoms from McMurdo Sound, Antarctica. *J. Phycol.*, 27: 367-373.

Matsumoto, G.I. 1989. Biogeochemical study of organic substances in Antarctic lakes. *Hydrobiologia* 172: 265-289.

Masuda, N., Nakaya, S., Burton, H.R., and T. Torii, 1988. Trace element distributions in some saline lakes of the Vestfold Hills, Antarctica. In: Ferris, J.M., Burton, H.R., Johnstone, G.W., and I.A.E. Bayly (Eds)., *Biology of the Vestfold Hills: Proceedings of the Symposium, Hobart, August, 1984. Hydrobiologica 165* and *Developements in Hydrobiologica 34.* Kluwer Academic Publishers, Dordrecht. Pp. 103-115.

Mancuso C.A., Franzmann, P.D., Burton, H.R. and P.D. Nichols 1990. Microbial Community Structure and Biomass Estimates of a metanogenic Antarctic lake Ecosystem as determined by Phospholipid analysis. Microb. Ecol. 19: 73-95

Mc Fadden, G. I., Hill, D. R. A. and Wetherbee, R., 1986. A study of the genus Pyramimonas (Prasinophyceae) from south-eastern Australia. *Nord. J. Bot.* 6: 209-234

McFadden, G. I., Moestrup, Ø. and Wetherbee, R., 1982. Pyramimonas gelidicola sp. nov. (Prasinophyceae), a new species isolated from Antarctic sea ice. *Phycologia*, **21**: 103-111.

McMinn, A. and Hodgeson, D. (in prep). Seasonal Phytoplankton succession in Ellis Fjord, Eastern Antarctica *Journel of Plankton Research.*

Mitchell, C., 1990. Photosynthetic Physiology of Antarctic Sea-Ice Microalgae. unpub.*PhD Thesis*, School of Botany, University of Melbourne, Australia. pp 35

Morel, F. M., Rueter, J. G., Anderson, D. M., and Guillard, R. R. L., 1979. Aquil: A Chemically defined Phytoplankton Culture Medium for Trace Metal Studies. *J Phycol,* **15**: 135-141.

Morgan, K. and Kallf, J., 1975. The winter dark survival of an algal flagellate Cryptomonas erosa (Skuja). *Verh. int. Ver. Limmol.*, **19**: 2734-2740.

Morita, R. Y., 1975. Psychrophillic bacteria. *Bacteriological Reviews*, **39**: 144-167.

Morris, I., Glover, H. E. and Yentsch, C. S., 1974. Products of photosynthesis by marine phytoplankon: the effect of environmental factors on the relative rates of protein synthesis. *Mar. Biol.* **27**: 1-9.

Ohmoto, K., 1983. The Problem and significance of Radiocarbon geochronology in Antarctica. In: R. L. Oliver, P. R. James and J. B. Jage (Editors), *Antarctic Earth Science.* Aust. Acad. Sci., Canberra, pp. 450-452.

Oppenheim, D., and G. J. F. Pugh, 1987. A checklist of marine diatoms found on wood blocks exposed in the littoral environment of Signy Island, South Orkney Islands. *Br Ant Sur Bull77,* 161-171.

Palmisano, A. C., SooHoo, J. B. and Sullivan, C. W., 1987. Effects of four environmental variables on photosynthesis-irradience relationships in Antarctic sea ice microalgae. *Mar. Biol.* **94**: 299-306.

Palmisano, A. C. and Sullivan C. W. 1982. Physiology of sea ice diatoms. 1. Response of three polar diatoms to a simulated summer-winter transition. *J. Phycol,* **18**: 489-498.

Palmisano, A. C. and Sullivan C. W. 1985. Growth, metabolism and dark survival in sea ice microalgae. *New Phytol.*, **75**: 131-146

Pardue, J. W., Scanlan, R. S., Van Baalen, C. and Parker, P. L., 1976. Maximum carbon isotope fractionation in photosynthesis by blue green algae and a green algae. *Geochim. Cosmochim. Acta,* **40**: 309-312

Parke, M., 1949. Studies on marien flagellates. *J. Mar. Biol. Assoc. U. K.* **28**: 255-186.

Parke, M. and den Hartog-Adams, I., 1965. Three species of Halosphaera. *J. Mar. Biol. Assoc. U. K.* **45**: 537-557.

Parker, B. C., Hoehn, R.C., Paterson, R.A., Craft, J.A., Lane, L.S., Stavros, R.W., Sugg, H.G., Whitehurst, J.T., Fortner, R.D., and B.L. Weand, 1977. Changes in dissolved organic matter, photosynthetic production and microbiol community composition in Lake Bonney, Southern Victoria Land, Antarctica. In: Llano, G.A., (ed.). *Adaptions within Antarctic ecosystems.* Smithsonian Institution, Washington B.C.

Parker, N. S., 1992. Southern Ocean Phytoplankton: A Study of Community Structure. *Honours Thesis,* IASOS, University of Tasmania, Australia.

Perrin, R. A., Lu, P. and Marchant, H. J., 1987. Seasonal variation in marine phytoplankton and ice algae at a shallow antarctic coastal site. *Hydrobiologia* **146**: 33-46.

Peterson, J. A., Findlayson, B. L. and Qingsong, Z., 1988. Changing Distribution of late Quarternary lacustrine and littoral environments in the Vestfold Hills, Antarctica. *Hydrobiologia,* **165**: 221-226.

Pichon, J. J., Labeyrie, L.D., Bareille, G., Labracherie, M., Duprat, J. and Jouzel, J., 1992. Surface Water Temperature changes in the High Latitudes of the Southern Hemisphere over the Last Glacial-Interglacial Cycle. *Paleoceanography.* **7**: 289-318.

Pickard, J., 1983. Surface lowering of ice-cored moraine by wandering lakes. *J Glaciol.*, 29: 338-342.

Pickard, J., 1986. Antarctic oases, Davis station and the Vestfold Hills. In: J. Pickard (Editor), *Antarctic Oasis*. Academic Press, Sydney, pp. 1-19.

Pickard, J., Adamson, D. A. and Heath, C. W., 1986. The evolution of Watts Lake, Vestfold Hills, East Antarctica, from marine inlet to freshwater lake. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 53: 271-288.

Pienaar, R.N. and Aken, M.E., 1985. Preliminary investigations on the chemical composition of the scale boundary and cyst wall of Pyramimonas pseudoparkeae (Prasinophyceae). *S. Afr. J. Bot.*, 51: 408-416.

Pook, M. J., 1989. Variability of the Mid-Tropospheric flow over the Southern ocean and possible associations. *Honours Thesis*, IASOS, University of Tasmania, Australia.

Poulin, M., Cardinal, A. and Legendre, L., 1983. Response of a community of sea ice diatoms to a salinity gradient (Hudson Bay). *Mar. Biol.*, 76: 191-202.

Priscu, J. C, Priscu, L. R., Palmisano, A. C and Sullivan, C. W., 1987. The effect of temperature on inorganic nitrogen and carbon metabolism in sea ice microalgae. *Antarct. J. U. S.*, 22: 196-198.

Quilty, P. G., 1985. Australia's Antarctic Basins-Identification and Evolution. The 1985 PESA Australian Distinguished Lecture. *PESA Journal*, 8: 20-46.

Riley, J. P. and Chester, R., 1971. *Introduction to Marine Chemistry*. Academic Press, Lond. 265pp

Rochet, M., Lengendre, L. and Demers, S., 1986. Photosynthetic and pigment responses of sea ice microalgae, to changes in light intensity and quaility. *J. Exp. Mar. Biol. Ecol.*, 101: 211-226

Schmarda, L. K., 1850. Neue Formen von Infusorien. *Denkschr. Akad. Wiss. Wien*, 1: 9-14

Smayda, T. J., 1969. Experimental observations on the influence of temperature, light and salinity on cell division of the marine diatom, Detonula confervacea (Cleve) Gran. *J. Phycol*, 5: 150-157.

Smith Jnr., W. O., Keene, N. K. and Cosmiso, J. C., 1988. Interannual Variability in Estimated Primary Productivity of the Antarctic Marginal Ice Zone. In: Sahrhage,D (ed). *Antarctic Ocean and Resources Variability*. Springer-Verlag, Berlin pg. 131-138.

Solopav, A. V., 1969. *Oases in Antarctica.* (Division of Polar programs, National Science Foundation Technical Translation TT 68-50490)

SooHoo, J. B., Lizotte, M. P., Robinson, D. H., and Sullivan, C.W., 1987. AMERIEZ 1986: Photoadaption of phytoplankton and light limitation of primary production in the ice dge zone of the Weddell Sea. *Ant. J. U.S*,.22(5)

Stockwell, D. A., Kang, S-H, and Fryxell, G., 1991. Comparisions of Diatom Biocoenoses with Holocene Sediment Assemblages in Prydz Bay, Antarctica. Proceedings of the ocean drilling program. Scientific results, Vol 119: 667.

Streten N. A., 1986. Climate of the Vestfold Hills. In: J. Pickard (Editor), *Antarctic Oasis.* Academic Press, Sydney, pp. 141-164.

Tucker, M. J., 1983. The zooplankton and ice-water interface fauna of the inshore marine area of the Vestfold Hills, Antarctica. B.Sc. (Honours) Thesis, Univ. of Tasmania, Hobart, Australia, pp. 90.

van den Hoff, J., Burton, H. R. and Vesk, M., 1989. An encystment stage, bearing a new scale type, of the Antarctic Prasinophyte Pyramimonas gelidicola and it's palaeolimnological and taxonomic significance. *J. Phycol.*, 25: 446-454.

Vargo, G. A., Fanning, K., Heil, C. and Bell, L., 1986. Growth rates and the salinity response of an Antarctic Ice Microflora Community. *Polar Biology.*, 5: 241-247.

Volkman, J. K., Allen, D. I., Stevenson, P. L. and Burton, H. R., 1986. Bacterial and Algal hydrocarbons in sediments from a saline Antarctic lake, Ace Lake. *Organic Geochem.*, 10: 671-681

Verity, P. G., Villareal, T. A. and Smayda, T. J., 1988. Ecological investigations of blooms of colonial Phaeocystis pouchetti. Abundance, biochemical composition and metabolic rates. *J. Plankton Res.*, 10: 219-248.

Volkmann, J. K., Burton, H. R., Everitt, D. A. and Allen, D. I., 1988. Pigment and Lipid compositions of Algal and Bacterial communities in Ace Lake, Vestfold Hills, Antarctica. *Hydrobiologia*, 165: 41-57

Warnke, D. A., Richter, J. and Oppenheimer, C. H., 1973. Characteristics of the near shore environment off the south coast of Anvers Island, Antarctic peninsula. *Limmnol. Oceanogr.*, 18: 131-142.

Wasell, A. and Hakansson, H., 1992. Diatom stratigraphy in a lake on Horseshoe Island, Antarctica: A Marine-Brackish-Fresh water tansition with comments on the systematics and ecology of the most comman diatoms. *Diatom Res.*, 7: 157-194.

Wharton Jnr., R. A., Parker, B. C. and Simmons Jnr, G. M., 1983. Distribution, species compsition, and morphology of Algal mats inAntarctic Dry Valley Lakes. *Phycologia*, 22: 355-365.

Wright, S.W., and Burton, H.R., 1981. The biology of Antarctic saline lakes. *Hydrobiologia 82,* 319-338.

Zhang, Q., Xie, Y. and Li, Y., 1983. A Preliminary Study of the Evolution of the post late Pleistocene Vestfold Hills environment, East Antarctica. In: R. L. Oliver, P. R. James and J. B. Jage (Editors), *Antarctic Earth Science.* Aust. Acad. Sci., Canberra, pp. 473-477.

Appendix

Appendix 1

Diatom Stratigraphy Data

Depth (cms)	Years B.P. (uncorrected)	Other Species	Std Error	% of Total	P. microstauron	Std Error	% of Total	Stauroneis sp.	Std Error
0.00	0.00								
2.50	481.82	271.00	2.00	86.22	3.67	0.88	1.17	38.33	3.84
7.50	1445.45	271.67	9.84	83.93	11.33	0.33	3.50	32.33	2.73
12.50	2409.09	278.33	2.40	84.86	20.67	3.18	6.30	26.67	6.98
17.50	3372.73	235.00	10.69	75.48	26.67	2.91	8.57	45.00	3.61
22.50	4336.36								
27.50	5300.00	231.00	2.08	71.37	0.00	0.00	0.00	19.00	5.86
32.50	5365.45	237.00	7.02	74.61	3.33	0.33	1.05	12.67	0.88
37.50	5430.91	229.33	3.93	69.64	0.00	0.00	0.00	1.33	0.67
42.50	5496.36	280.67	7.33	79.51	0.33	0.33	0.09	0.33	0.33
47.50	5561.82	214.67	2.40	68.88	0.00	0.00	0.00	0.67	0.67
52.50	5627.27	222.67	18.02	69.58	0.00	0.00	0.00	0.67	0.67
57.50	5692.73	188.33	13.13	57.71	0.00	0.00	0.00	0.33	0.33
62.50	5758.18	197.67	13.54	61.90	0.00	0.00	0.00	0.00	0.00
67.50	5823.64	202.67	5.81	62.17	0.00	0.00	0.00	0.00	0.00
72.50	5889.09	237.00	7.64	73.68	0.00	0.00	0.00	0.00	0.00
77.50	5954.55	190.00	5.57	60.64	0.00	0.00	0.00	0.00	0.00
82.50	6020.00	202.67	4.84	65.17	0.00	0.00	0.00	0.00	0.00
87.50	6085.45	225.00	5.69	71.20	0.00	0.00	0.00	0.00	0.00
92.50	6150.91	247.33	2.03	79.10	0.00	0.00	0.00	0.00	0.00
97.50	6216.36	204.33	33.27	73.85	0.00	0.00	0.00	1.67	0.88
102.50	6281.82	243.33	10.90	77.58	0.00	0.00	0.00	1.00	0.58
107.50	6347.27	264.00	3.61	83.99	0.00	0.00	0.00	0.33	0.33
112.50	6412.73	247.67	14.72	80.76	0.00	0.00	0.00	0.00	0.00
117.50	6478.18	241.67	2.96	78.29	0.00	0.00	0.00	0.67	0.67
122.50	6543.64	249.67	11.02	78.84	0.00	0.00	0.00	1.33	0.88
127.50	6609.09	259.00	11.53	80.52	0.00	0.00	0.00	8.00	3.21
132.50	6674.55	267.33	2.60	87.17	0.00	0.00	0.00	11.00	2.52
137.50	6740.00	35.00	7.81	15.86	120.33	5.90	54.53	65.00	16.09
142.50	7013.34	18.00	2.00	11.97	129.33	6.96	86.03	2.67	2.67
147.50	7286.67	13.00	2.00	25.33	34.00	4.73	66.24	4.00	1.00
152.50	7560.01	19.33	1.67	29.44	41.67	4.48	63.45	4.33	3.38
157.50	7833.34	12.33	2.19	30.83	27.00	4.58	67.50	0.67	0.67
162.50	8106.68	5.67	1.20	54.89	4.33	0.88	41.92	0.00	0.00
167.50	8380.00	11.33	0.67	53.95	4.33	1.33	20.62	4.00	1.00
172.50	8653.35	233.00	12.58	71.99	0.00	0.00	0.00	1.00	1.00
177.50	8926.68	53.00	5.20	79.90	0.00	0.00	0.00	1.67	1.20
182.50	9200.02	63.00	15.31	64.95	2.00	2.00	2.06	5.00	1.53

Appendix 1

Diatom Stratigraphy Data

% of Total	% Freshwater	N. curta	Std Error	% of Total	N. cyclindrus	Std Error	% of Total	% Pioneer sp.	E. antarctica	Std Error
12.19	13.36	0.00	0.00	0.00	1.33	0.88	0.42	0.42	0.00	0.00
9.99	13.49	5.67	1.20	1.75	2.00	0.58	0.62	2.37	0.00	0.00
8.13	14.43	0.00	0.00	0.00	2.33	0.67	0.71	0.71	0.00	0.00
14.45	23.02	1.00	0.58	0.32	3.00	0.58	0.96	1.28	0.00	0.00
5.87	5.87	13.67	1.20	4.22	38.33	3.18	11.84	16.07	0.00	0.00
3.99	5.04	16.33	2.40	5.14	41.33	2.40	13.01	18.15	0.00	0.00
0.40	0.40	22.67	5.24	6.88	65.67	5.36	19.94	26.82	0.33	0.33
0.09	0.19	13.00	2.89	3.68	55.67	5.78	15.77	19.45	0.00	0.00
0.21	0.21	19.00	1.53	6.10	75.67	5.93	24.28	30.38	0.33	0.33
0.21	0.21	19.00	7.64	5.94	73.33	6.74	22.92	28.85	0.00	0.00
0.10	0.10	23.33	7.31	7.15	108.33	5.24	33.20	40.35	0.00	0.00
0.00	0.00	17.67	4.91	5.53	98.67	5.70	30.90	36.43	1.00	0.58
0.00	0.00	25.67	3.71	7.87	89.00	3.61	27.30	35.17	1.67	0.88
0.00	0.00	18.00	2.31	5.60	62.33	3.48	19.38	24.97	1.00	0.00
0.00	0.00	20.67	4.67	6.60	95.00	1.53	30.32	36.92	0.67	0.67
0.00	0.00	21.67	2.91	6.97	79.33	5.04	25.51	32.48	1.33	0.88
0.00	0.00	21.00	2.89	6.65	64.33	5.24	20.36	27.00	0.67	0.33
0.00	0.00	7.00	0.58	2.24	44.67	1.45	14.29	16.53	1.67	0.67
0.60	0.60	13.00	2.52	4.70	44.33	4.41	16.02	20.72	1.33	0.67
0.32	0.32	16.33	3.48	5.21	40.67	3.18	12.97	18.17	1.00	0.58
0.10	0.10	8.00	1.53	2.55	35.00	3.79	11.13	13.68	1.67	0.88
0.00	0.00	13.33	2.33	4.35	37.33	11.29	12.17	16.52	1.67	0.88
0.22	0.22	7.33	2.60	2.37	47.00	6.08	15.23	17.60	0.00	0.00
0.42	0.42	15.00	3.51	4.74	39.33	10.93	12.42	17.16	0.00	0.00
2.49	2.49	11.00	1.53	3.42	33.00	8.62	10.26	13.68	0.67	0.33
3.59	3.59	3.33	1.45	1.09	20.00	1.00	6.52	7.61	0.00	0.00
29.46	83.99	0.00	0.00	0.00	0.33	0.33	0.15	0.15	0.00	0.00
1.78	87.81	0.00	0.00	0.00	0.33	0.33	0.22	0.22	0.00	0.00
7.79	74.03	0.00	0.00	0.00	0.33	0.33	0.64	0.64	0.00	0.00
6.59	70.05	0.00	0.00	0.00	0.33	0.33	0.50	0.50	0.00	0.00
1.68	69.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	41.92	0.00	0.00	0.00	0.33	0.33	3.19	3.19	0.00	0.00
19.05	39.67	0.33	0.33	1.57	1.00	0.58	4.76	6.33	0.00	0.00
0.31	0.31	7.33	0.88	2.26	78.00	3.79	24.10	26.36	0.33	0.33
2.52	2.52	0.00	0.00	0.00	6.33	2.85	9.54	9.54	0.00	0.00
5.15	7.22	8.33	0.33	8.59	12.00	2.08	12.37	20.96	0.00	0.00

Appendix 1

Diatom Stratigraphy Data

% of Total	Centric	Std Error	% of Total	% Open Marine	Total Cells
0.00	0.00	0.00	0.00	0.00	314.33
0.00	0.67	0.67	0.21	0.21	323.67
0.00	0.00	0.00	0.00	0.00	328.00
0.00	0.67	0.33	0.22	0.22	311.33
0.00	21.67	4.70	6.70	6.70	323.67
0.00	7.00	0.58	2.20	2.20	317.67
0.10	10.00	2.52	3.04	3.14	329.33
0.00	3.00	1.00	0.85	0.85	353.00
0.11	1.33	0.67	0.43	0.53	311.67
0.00	4.33	1.33	1.35	1.35	320.00
0.00	6.00	1.15	1.84	1.84	326.33
0.31	4.33	1.20	1.36	1.67	319.33
0.51	7.00	0.58	2.15	2.66	326.00
0.31	3.33	0.88	1.04	1.35	321.67
0.21	7.00	0.58	2.23	2.45	313.33
0.43	6.00	1.15	1.93	2.36	311.00
0.21	5.00	1.00	1.58	1.79	316.00
0.53	12.00	0.58	3.84	4.37	312.67
0.48	12.00	1.73	4.34	4.82	276.67
0.32	11.33	1.76	3.61	3.93	313.67
0.53	5.33	0.67	1.70	2.23	314.33
0.54	6.67	0.67	2.17	2.72	306.67
0.00	12.00	2.65	3.89	3.89	308.67
0.00	11.33	2.91	3.58	3.58	316.67
0.21	10.00	2.08	3.11	3.32	321.67
0.00	5.00	1.00	1.63	1.63	306.67
0.00	0.00	0.00	0.00	0.00	220.67
0.00	0.00	0.00	0.00	0.00	150.33
0.00	0.00	0.00	0.00	0.00	51.33
0.00	0.00	0.00	0.00	0.00	65.67
0.00	0.00	0.00	0.00	0.00	40.00
0.00	0.00	0.00	0.00	0.00	10.33
0.00	0.00	0.00	0.00	0.00	21.00
0.10	4.00	0.58	1.24	1.34	323.67
0.00	5.33	1.20	8.04	8.04	66.33
0.00	6.67	2.33	6.88	6.88	97.00

Appendix 2

Pyramimonas gelidicola scale concentrations in an Ace Lake sediment core

Depth (cms)	Years (uncorrected)	Mean Body Scale/FOV	Std err. Body scale	Cyst Scale/FOV at x20K
2.5	481.82	3.83	0.40	0
7.5	1445.45	1.57	0.38	0
12.5	2409.09	21.8	0.12	0
17.5	3372.73	6.17	0.09	0
22.5	4336.36			
27.5	5300	2.9	0.39	0
32.5	5365.45			
37.5	5430.91	0.6	0.17	0
42.5	5496.36			
47.5	5561.82	0.37	0.16	1
52.5	5627.27	0.13	0.43	0
57.5	5692.73	0.07	0.87	0
62.5	5758.18			
67.5	5823.64	0.03	1.73	0
72.5	5889.09	0.1	0.00	0
77.5	5954.55	0.37	0.31	2
82.5	6020	0.3	1.00	0
87.5	6085.45	0.4	0.25	0
92.5	6150.91	6.97	0.05	5
97.5	6216.36	1.03	0.15	2
102.5	6281.82	0.27	0.57	0
107.5	6347.27	2.87	0.17	10
112.5	6412.73	0	0.00	0
117.5	6478.18	0.87	0.18	0
122.5	6543.64	8.01	0.23	4
127.5	6609.09	2.43	0.40	6
132.5	6674.55	0.43	0.74	0
137.5	6740	4.47	0.46	2
142.5	7013.34	2.73	0.32	2
147.5	7286.67	1.2	0.65	1
152.5	7560.01	0.23	0.25	0
157.5	7833.34	3.33	0.49	0
162.5	8106.68	0.1	1.73	0
167.5	8380	0.23	0.65	0
172.5	8653.35	0.17	0.35	0
177.5	8926.68	1.07	0.20	0
182.5	9200.02	0.77	0.20	0

Cell and Cyst production of the Prydz Bay strain of Pyramimonas gelidicola in different temperature treatments

Age (Days)	Cell no. -1.5°C	Cyst no. -1.5°C	Cell no. -0.5°C	Cyst no. -0.5°C	Cell no. 1.5°C	Cyst no. 1.5°C	Cell no. 2°C	Cyst no. 2°C
0	24000	0	24000	0	24000	0	24000	0
2	40830	833.33	37500	1666.67	30830	2500	32500	833.33
4	27500	1666.67	20830	833.33	25830	0	23330	0
6	35830	0	35830	0	35830	0	31670	1666.67
8	40830	0	38330	3333.33	45830	0	81670	2500
10	43330	4166.67	80830	0	65000	0	74170	0
12	65830	3333.33	106670	0	81670	0	120000	0
14	75000	833.33	109170	2500	101670	0	121670	0
16	102500	833.33	126670	833.33	135000	0	156670	0
18	128330	2500	180000	1666.67	135000	0	110830	0
20	126670	0	135000	4166.67	154170	1666.67	130000	0
22	145000	1666.67	169170	2500	174170	0	160000	0
24	136670	1666.67	155830	0	180000	5000	135830	1666.67
26	140000	1666.67	149170	0	139170	0	116670	0
28	133330	0	114170	833.33	120000	1666.67	128330	0
30	146670	0	125830	833.33	111670	3333.33	153330	1666.67
32	157500	4166.67						
34	140830	4166.67						

Cell and Cyst production of the Prydz Bay strain of Pyramimonas gelidicola in different temperature treatments

Cell no. 3°C	Cyst no. 3°C	Cell no. 4°C	Cyst no. 4°C	Cell no. 5°C	Cyst no. 5°C	Cell no. 6°C	Cyst no. 6°C	Cell no. 7°C
24000	0	24000	0	24000	0	24000	0	24000
19170	0	21670	2500	48330	833.33	35000	1666.67	32500
26670	833.33	32500	0	33330	833.33	40000	2500	30830
38330	0	30000	0	40830	833.33	29170	833.33	53330
51670	2500	39170	4166.67	42500	833.33	46670	833.33	56670
70000	0	44170	0	97500	1666.67	130000	833.33	107500
100830	1666.67	87500	1666.67	98330	1666.67	85830	833.33	120830
117500	3333.33	124170	3333.33	129170	2500	135000	3333.33	132500
106670	0	139170	3333.33	133330	4166.67	163330	1666.67	135000
136670	833.33	115830	1666.67	172500	0	120000	833.33	172500
127500	0	107500	2500	122500	833.33	126670	3333.33	141670
135830	2500	126670	0	135830	1666.67	170000	833.33	160830
134170	2500	115830	0	115830	3333.33	144170	3333.33	124170
117500	0	102500	0	115830	0	130830	0	104170
128330	1666.67	97500	1666.67	102500	0	142500	0	118330
138330	0	105000	833.33	99170	1666.67	115830	833.33	118330

Cell and Cyst production of the Prydz Bay strain of Pyramimonas gelidicola in different temperature treatments

Cyst no. 7°C	Cell no. 8°C	Cyst no. 8°C	Cell no. 9°C	Cyst no. 9°C	Cell no. 10°C	Cyst no.10°C	Cell no. 11°C	Cyst no. 11°C
0	24000	0	24000	0	24000	0	24000	0
0	42500	1666.67	48330	0	48330	1666.67	31670	833.33
0	25000	3333.33	48330	0	41670	0	30830	833.33
1666.67	44170	833.33	41670	0	45000	833.33	44170	833.33
833.33	64170	0	68330	4166.67	92500	833.33	55830	0
0	100000	1666.67	96670	1666.67	139170	4166.67	81670	2500
833.33	122500	1666.67	105830	1666.67	97500	3333.33	70830	3333.33
833.33	125000	0	148330	1666.67	176670	5000	98330	2500
1666.67	151670	3333.33	157500	2500	173330	6666.67	108330	4166.67
0	150000	833.33	164170	0	126670	0	110000	1666.67
0	146670	1666.67	137500	833.33	139170	2500	126670	3333.33
1666.67	168330	1666.67	165000	0	166670	3333.33	112500	5000
0	148330	1666.67	122500	0	135830	3333.33	127500	833.33
833.33	194170	1666.67	93330	833.33	131670	0	126670	4166.67
2500	124170	1666.67	100000	833.33	108330	1666.67	105830	2500
2500	131670	0	111670	0	84170	1666.67	110000	0

Cell and Cyst production of the Prydz Bay strain of Pyramimonas gelidicola in different temperature treatments

Cell no.12°C	Cyst no. 12°C	Cell no.13°C	Cyst no.13°C	Cell no.14°C	Cyst no.14°C	Cell no.15°C	Cyst no.15°C	Cell no.16°C
24000	0	24000	0	24000	0	24000	0	24000
23330	0	49170	1666.67	46670	2500	22500	0	43330
26670	0	35830	833.33	23330	1666.67	24170	833.33	15830
34170	1666.67	36670	833.33	31670	3333.33	28330	0	14170
54170	3333.33	50830	3333.33	24170	2500	15830	833.33	18330
50000	2500	62500	833.33	45830	2500	29170	833.33	16670
80830	833.33	68330	3333.33	50000	1666.67	20830	0	10000
94170	3333.33	70000	833.33	61670	833.33	24170	1666.67	20830
91670	1666.67	76670	833.33	47500	0	28330	0	14170
105000	0	86670	0	55000	833.33	30830	1666.67	20000
106670	0	83330	0	56670	3333.33	30000	0	10830
101670	5000	80830	1666.67	36670	1666.67	28330	4166.67	12500
100000	833.33	99170	2500	67500	833.33	23330	3333.33	7500
73330	1666.67	77500	2500	65830	5000	22500	4166.67	5830
78330	833.33	69170	1666.67	37500	833.33	40830	0	9170
90830	833.33	71670	4166.67	54170	1666.67	22500	833.33	1670

Cell and Cyst production of the Prydz Bay strain of Pyramimonas gelidicola in different temperature treatments

Cyst no.16°C	Cell no.17°C	Cyst no.17°C	Cell no.18°C	Cyst no. 18°C
0	24000	0	24000	0
2500	25000	0	49170	2500
0	20000	833.33	20000	0
4166.67	14170	2500	20830	0
1666.67	16670	0	31670	0
833.33	7500	833.33	21670	833.33
0	7500	833.33	25830	833.33
1666.67	5830	0	10000	0
0	13330	0	10000	0
833.33	10000	833.33	5830	0
833.33	7500	0	5000	0
833.33	8330	833.33	3330	0
0	5830	0	1670	833.33
0	1670	0	830	0
0	7500	0	2500	0
0	6670	2500	830	0

Cell and Cyst production of the Ace Lake strain of Pyramimonas gelidicola in different Temperature treatments

Age (Days)	Cells no. -1.5°C	Cyst no. -1.5	Cells no. -0.5°C	Cyst no. -0.5	Cells no. 1.5°C	Cyst no. 1.5	Cells no. 2°C	Cyst no. 2°C	Cells no. 3°C	Cyst no. 3°C	Cells no. 4°C	Cyst no. 4°C	Cells no. 5°C
0	34166.6667	0	34166.6667	0	34166.6667	0	34166.6667	0	34166.6667	0	34166.6667	0	34166.6667
2	35000	833.333333	30833.3333	0	49166.6667	0	32500	0	52500	0	46666.6667	0	30833.3333
4	32500	833.333333	43333.3333	0	31666.6667	0	26666.6667	0	48333.3333	0	42500	0	31666.6667
6	62500	0	65833.3333	0	47500	1666.66667	68333.3333	0	56666.6667	0	60000	0	85000
8	56666.6667	833.333333	53333.3333	0	67500	0	70000	833.333333	115000	4166.66667	72500	833.333333	69166.6667
10	75833.3333	0	68333.3333	833.333333	93333.3333	833.333333	90833.3333	0	87500	833.333333	94166.6667	0	108333.333
12	100833.333	0	110000	0	87500	0	91666.6667	0	95000	833.333333	105000	0	125000
14	169166.667	0	118333.333	0	104166.667	0	121666.667	0	77500	0	106666.667	0	103333.333
16	126666.667	0	124166.667	0	82500	0	99166.6667	0	73333.3333	0	96666.6667	0	139166.667
18	179166.667	0	96666.6667	0	95833.3333	0	100000	0	75000	0	90833.3333	0	126666.667
20	187500	0	127500	0	116666.667	0	125000	0	98333.3333	833.333333	104166.667	0	138333.333
22	120833.333	0	107500	0	120000	0	128333.333	0	90000	0	115000	0	141666.667
24	164166.667	0	127500	0	113333.333	0	123333.333	0	84166.6667	0	96666.6667	0	105000
26	96666.6667	0	128333.333	0	108333.333	0	116666.667	0	82500	0	90000	0	91666.6667
28	160000	0	130000	1666.66667	115833.333	0	121666.667	0	70000	0	80000	0	78333.3333
30	106666.667	0	123333.333	0	105833.333	0	104166.667	0	75000	0	70833.3333	0	79166.6667
32	97500	0	110000	0	91666.6667	0	88333.3333	0	42500	0	53333.3333	0	68333.3333

Cell and Cyst production of the Ace Lake strain of Pyramimonas gelidicola in different Temperature treatments

Cyst 5	Cells no. 6°C	Cyst no. 6°C	Cells no. 7°C	Cyst 7	Cells no. 8°C	Cyst no. 8°C	Cells no. 9°C	Cyst no. 9°C	Cells no. 10°C	Cyst no. 10°C	Cells no. 11°C	Cyst no. 11°C	Cells no. 12°C
0	34166.6667	0	34166.6667	0	34166.6667	0	34166.6667	0	34166.6667	0	34166.6667	0	34166.6667
0	41666.6667	0	57500	0	43333.3333	0	28333.3333	0	40833.3333	0	39166.6667	0	34166.6667
0	48333.3333	0	75833.3333	0	69166.6667	0	53333.3333	0	60000	0	70000	0	58333.3333
0	84166.6667	0	79166.6667	833.333333	103333.333	833.333333	81666.6667	0	122500	0	82500	0	90000
0	129166.667	0	102500	0	123333.333	0	90000	833.333333	86666.6667	0	98333.3333	0	110000
0	106666.667	0	165833.333	0	152500	0	102500	0	120000	0	111666.667	0	108333.333
0	110833.333	0	139166.667	0	154166.667	0	114166.667	0	166666.667	0	102500	0	107500
0	131666.667	0	162500	0	173333.333	0	126666.667	0	180833.333	0	120833.333	0	111666.667
0	161666.667	0	165000	0	187500	0	148333.333	0	140000	0	131666.667	0	99166.6667
0	148333.333	0	215000	0	195833.333	0	145833.333	0	215000	0	142500	0	90000
0	172500	0	245000	0	204166.667	0	135000	0	161666.667	0	127500	0	87500
0	176666.667	0	200000	0	146666.667	0	126666.667	0	149166.667	0	119166.667	0	86666.6667
0	179166.667	0	159166.667	0	172500	0	184166.667	0	165000	0	148333.333	0	73333.3333
0	222500	0	150000	0	192500	0	142500	0	156666.667	0	133333.333	0	64166.6667
0	179166.667	0	140833.333	0	156666.667	0	135000	0	145833.333	0	123333.333	0	61666.6667
0	151666.667	0	123333.333	0	142500	0	121666.667	0	145833.333	0	104166.667	0	46666.6667
0	145833.333	0	108333.333	0	135833.333	0	110000	0	133333.333	0	90833.3333	0	34166.6667

Cell and Cyst production of the Ace Lake strain of Pyramimonas gelidicola in different Temperature treatments

Cyst no.12°C	Cells no. 13°C	Cyst no.13°C	Cells no.14°C	Cyst no.14°C	Cells no. 15°C	Cyst no.15°C	Cells no. 16°C	Cyst no. 16°C	Cells no. 17°C	Cyst no.17°C	Cells no. 18°C	Cyst no. 18°C
0	34166.6667	0	34166.6667	0	34166.6667	0	34166.6667	0	34166.6667	0	34166.6667	0
0	31666.6667	0	36666.6667	0	41666.6667	0	42500	0	37500	0	30000	0
0	38333.3333	1666.66667	33333.3333	0	34166.6667	0	40833.3333	833.333333	30000	0	30833.3333	0
0	69166.6667	0	40000	1666.6667	43333.3333	833.333333	34166.6667	833.333333	30000	1666.66667	24166.6667	0
833.333333	63333.3333	833.333333	42500	0	30000	833.333333	22500	0	38333.3333	0	19166.6667	0
833.333333	79166.6667	0	43333.3333	0	40833.3333	0	10833.3333	833.333333	29166.6667	0	11666.6667	0
833.333333	58333.3333	0	62500	0	30833.3333	0	9166.6667	0	25833.3333	0	11666.6667	0
833.333333	67500	0	49166.6667	0	26666.6667	0	9166.6667	0	7500	833.333333	20833.3333	0
0	75833.3333	0	64166.6667	0	24166.6667	0	6666.6667	0	10000	0	3333.3333	0
0	77500	0	63333.3333	0	20833.3333	0	5833.3333	0	14166.6667	0	2500	0
0	82500	0	50833.3333	0	19166.6667	0	5833.3333	0	6666.6667	0	2500	0
0	88333.3333	0	50000	0	15000	0	5833.3333	0	6666.6667	0	1666.6667	0
0	105000	0	41666.6667	0	9166.667	0	416.6667	0	5833.3333	0	833.3333	0
0	90000	0	38333.3333	0	8333.3333	0	3333.3333	0	5833.3333	0	833.3333	0
0	78333.3333	0	32500	0	6666.6667	0	2500	0	4166.6667	0		
0	56666.6667	0	26666.6667	0	4166.6667	0	1666.6667	0	2500	0		
0	49166.6667	0	22500	0	2500	0	833.3333	0				

Cell and Cyst production of the Prydz Bay strain of Pyramimonas gelidicola in different salinity treatments.

Age (Days)	Cell no. 5 ppt	Cyst no. 5 ppt	Cell no. 10 ppt	Cyst no. 10 ppt	Cell no. 15 ppt	Cyst no. 15 ppt
0.00	8181.82	0.00	8181.82	0.00	8181.82	0.00
2.00	4166.67	0.00	833.33	0.00	3333.33	0.00
4.00	2500.00	0.00	10000.00	0.00	3333.33	0.00
6.00	5833.33	0.00	10833.33	833.33	3333.33	0.00
8.00	7500.00	0.00	15000.00	0.00	9166.67	0.00
10.00	4166.67	0.00	20000.00	0.00	10833.33	0.00
12.00	11666.67	0.00	38333.33	0.00	22500.00	0.00
14.00	20000.00	0.00	70833.33	0.00	37500.00	0.00
16.00	22500.00	0.00	78333.33	0.00	54166.67	0.00
18.00	43333.33	0.00	83333.33	0.00	60000.00	0.00
20.00	29166.67	0.00	46666.67	0.00	72500.00	0.00
22.00	28333.33	0.00	40000.00	0.00	63333.33	0.00
24.00	30000.00	0.00	49166.67	0.00	94166.67	0.00
26.00	35833.33	0.00	49166.67	0.00	67500.00	0.00
28.00	16666.67	0.00	40000.00	0.00	48333.33	0.00
30.00	15000.00	0.00	27500.00	0.00	35833.33	0.00
32.00	13333.33	0.00	31666.67	0.00	40833.33	0.00
34.00	14166.67	0.00	37500.00	0.00	45833.33	0.00
36.00	26666.67	0.00	70833.33	0.00	50000.00	0.00
38.00	32500.00	0.00	61666.67	1666.67	89166.67	0.00
40.00	30000.00	0.00	55833.33	0.00	66666.67	0.00
42.00	35833.33	0.00	64166.67	0.00	61666.67	0.00
44.00	30000.00	0.00	58333.33	0.00	52500.00	0.00
46.00	29166.67	0.00	53333.33	0.00	54166.67	0.00
48.00						
50.00						
52.00						
54.00						
56.00						
58.00						
60.00						
62.00						
64.00						
66.00						
68.00						
70.00						
72.00						
77.00						
79.00						
83.00						
85.00						
87.00						
91.00						
93.00						
99.00						
101.00						

Cell and Cyst production of the Prydz Bay strain of Pyramimonas gelidicola in different salinity treatments.

Cell no. 20 ppt	Cyst no. 20 ppt	Cell no. 30 ppt	Cyst no. 30 ppt	Cell no. 35 ppt	Cyst no. 35 ppt	Cell no. 40 ppt
8181.82	0.00	8181.82	0.00	8181.82	0.00	8181.82
3333.33	0.00	4166.67	0.00	3333.33	0.00	5000.00
3333.33	0.00	5833.33	0.00	4166.67	0.00	2500.00
6666.67	0.00	7500.00	0.00	6666.67	0.00	2500.00
7500.00	0.00	5000.00	0.00	4166.67	0.00	2500.00
12500.00	0.00	8333.33	0.00	6666.67	0.00	10000.00
10833.33	0.00	10833.33	833.33	4166.67	0.00	10833.33
33333.33	0.00	22500.00	0.00	7500.00	0.00	8333.33
40000.00	0.00	14166.67	0.00	10000.00	0.00	11666.67
58333.33	0.00	12500.00	0.00	17500.00	0.00	19166.67
92500.00	0.00	23333.33	0.00	25833.33	0.00	27500.00
127500.00	0.00	37500.00	0.00	31666.67	0.00	33333.33
120833.33	0.00	39166.67	0.00	41666.67	0.00	29166.67
114166.67	0.00	53333.33	0.00	59166.67	0.00	56666.67
85000.00	0.00	72500.00	0.00	53333.33	0.00	74166.67
74166.67	0.00	91666.67	0.00	49166.67	0.00	77500.00
53333.33	0.00	120833.33	0.00	82500.00	833.33	93333.33
47500.00	0.00	155833.33	0.00	110833.33	0.00	136666.67
67500.00	0.00	149166.67	0.00	145833.33	833.33	179166.67
47500.00	0.00	169166.67	0.00	164166.67	0.00	190000.00
51666.67	0.00	151666.67	0.00	185000.00	0.00	210000.00
86666.67	0.00	153333.33	833.33	171666.67	0.00	195000.00
52500.00	0.00	150000.00	0.00	170833.33	0.00	190000.00
80833.33	0.00	116666.67	0.00	161666.67	0.00	155000.00
		125000.00	0.00	159166.67	0.00	160833.33
		115000.00	0.00	123333.33	0.00	146666.67
		87500.00	0.00	115000.00	0.00	132500.00
		74166.67	0.00	100833.33	0.00	129166.67

Cell and Cyst production of the Prydz Bay strain of Pyramimonas gelidicola in different salinity treatments.

Cyst no. 40 ppt	Cell no. 50 ppt	Cyst no. 50 ppt	Cell no. 60 ppt	Cyst no. 60 ppt	Cell no. 75 ppt	Cyst no. 75 ppt
0.00	8181.82	0.00	8181.82	0.00	8181.82	0.00
0.00	6666.67	833.33	5833.33	0.00	7500.00	0.00
0.00	4166.67	0.00	5000.00	0.00	5000.00	0.00
0.00	5833.33	833.33	5000.00	833.33	2500.00	0.00
0.00	5000.00	0.00	5000.00	0.00	4166.67	0.00
0.00	5833.33	0.00	5000.00	0.00	3333.33	0.00
0.00	2500.00	0.00	4166.67	0.00	833.33	0.00
0.00	3333.33	0.00	4166.67	0.00	2500.00	0.00
0.00	3333.33	0.00	6666.67	0.00	1666.67	0.00
0.00	2500.00	0.00	5000.00	0.00	1666.67	0.00
0.00	2500.00	0.00	5000.00	0.00	2500.00	0.00
0.00	2500.00	0.00	5000.00	0.00	1666.67	0.00
0.00	1666.67	0.00	7500.00	1666.67	1666.67	0.00
0.00	833.33	0.00	4166.67	833.33	833.33	0.00
0.00	1666.67	0.00	3333.33	0.00	833.33	0.00
0.00	0.00	0.00	833.33	0.00	0.00	0.00
0.00	833.00	0.00	833.30	0.00	0.00	0.00
0.00	0.00	0.00	833.30	0.00	833.30	0.00
0.00	0.00	0.00	833.30	0.00	833.30	0.00
833.33	3333.33	0.00	0.00	0.00	833.33	0.00
0.00	5000.00	0.00	0.00	0.00	1666.67	0.00
0.00	6666.67	0.00	68333.33	0.00	0.00	0.00
0.00	10833.33	0.00	56666.67	833.33	833.33	0.00
0.00	11666.67	0.00	54166.67	0.00	1666.67	0.00
0.00	42500.00	0.00	70000.00	0.00		
0.00	59166.67	0.00	75833.33	0.00		
0.00	95000.00	0.00	78333.33	0.00		
0.00	134166.67	0.00	90833.33	0.00		
	157500.00	0.00	117500.00	0.00		
	194166.67	0.00	110833.33	1666.67	0.00	0.00
	223333.33	0.00	107500.00	0.00	833.33	0.00
	196666.67	0.00	120000.00	0.00	833.33	0.00
	237500.00	0.00	139167.00	833.33	833.33	0.00
	208333.00	0.00	155000.00	0.00	0.00	0.00
	200833.00	0.00	161667.00	0.00	833.00	0.00
	192500.00	0.00	156667.00	1667.67	833.00	0.00
	195000.00	0.00	169167.00	0.00	1667.00	0.00
	80000.00	0.00	62500.00	0.00	833.00	0.00
	57500.00	0.00	65833.00	0.00	0.00	0.00
	53333.00	0.00	50000.00	0.00	0.00	0.00
	47500.00	0.00	51667.00	0.00		
	28333.00	0.00	36667.00	0.00		
	40833.00	0.00	44167.00	0.00		
	34167.00	0.00	34167.00	0.00	0.00	0.00
	30833.00	0.00	25833.00	0.00	0.00	0.00
	78333.00	0.00	85000.00	0.00	0.00	0.00

Cell and Cyst production of the Prydz Bay strain of Pyramimonas gelidicola in different salinity treatments.

Cell no. 80 ppt	Cyst no. 80 ppt	Cell no. 85 ppt	Cyst no. 85 ppt	Cell no. 90 ppt	Cyst no. 90 ppt	Cell no. 100 ppt
8181.82	0.00	8181.82	0.00	8181.82	0.00	8181.82
4166.67	833.33	2500.00	0.00	4166.67	0.00	2500.00
3333.33	0.00	500.00	0.00	3333.33	0.00	1666.67
3333.33	0.00	4167.00	0.00	3333.33	833.33	1666.67
2500.00	0.00	4167.00	0.00	1666.67	0.00	4166.67
833.33	0.00	4167.00	0.00	1666.67	0.00	1666.67
1666.67	0.00	1667.00	0.00	2500.00	0.00	0.00
833.33	0.00	2500.00	0.00	2500.00	0.00	0.00
833.33	0.00	1667.00	0.00	1666.67	0.00	0.00
833.33	0.00	1667.00	0.00	2500.00	0.00	0.00
1666.67	0.00	1667.00	0.00	1666.67	0.00	0.00
1666.67	0.00	1667.00	0.00	833.33	0.00	0.00
0.00	0.00	0.00	0.00	833.33	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00
833.30	0.00	0.00	0.00	0.00	0.00	0.00
833.30	0.00	0.00	0.00	0.00	0.00	0.00
833.33	0.00	833.00	0.00	0.00	0.00	0.00
0.00	0.00	833.00	0.00	0.00	0.00	0.00
0.00	0.00	833.33	0.00	0.00	0.00	0.00
833.33	0.00	1666.67	0.00	0.00	0.00	0.00
2500.00	0.00	1666.67	0.00	0.00	0.00	0.00
	0.00		0.00		0.00	
	0.00		0.00		0.00	
	0.00		0.00		0.00	
	0.00		0.00		0.00	
	0.00		0.00		0.00	
	0.00		0.00		0.00	
	0.00		0.00		0.00	
	0.00		0.00		0.00	
	0.00		0.00		0.00	
	0.00		0.00		0.00	
	0.00		0.00		0.00	

Cell and Cyst production of the Prydz Bay strain of Pyramimonas gelidicola in different salinity treatments.

Cyst no. 100 ppt
0.00
833.33
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00
0.00

Cell and Cyst production of the Ace Lake strain of Pyramimonas gelidicola in different salinity treatments

Age (Days)	Cell no. 5 ppt	Cyst no. 5 ppt	Cell no. 10 ppt	Cyst no. 10 ppt	Cell no. 15 ppt	Cyst no. 15 ppt
0	22000	0	22000	0	22000	0
2	25800	833.33	35800	0	32500	0
4	44200	0	49200	0	55000	833.33
6	60800	0	110000	0	110800	0
8	113300	833.33	140000	0	150000	0
10	80800	1666.67	150000	833.33	126700	833.33
12	108300	1666.67	123300	0	172500	0
14	119200	833.33	138300	0	193300	0
16	80000	0	115000	833.33	170800	1666.67
18	95800	833.33	139200	0	155000	833.33
20	109200	1666.67	110000	833.33	137500	3333.33
22	81700	833.33	112500	4166.67	120000	3333.33
24	75800	0	109200	833.33	128300	0
26	75000	3333.33	101700	4166.67	125800	0
28	77500	0	85800	1666.67	80800	4166.67
30	58300	0	89200	0	72500	3333.33

Cell and Cyst production of the Ace Lake strain of Pyramimonas gelidicola in different salinity treatments

Cell no. 20 ppt	Cyst no. 20 ppt	Cell no. 30 ppt	Cyst no. 30 ppt	Cell no. 35 ppt	Cyst no. 35 ppt	Cell no. 40 ppt
22000	0	22000	0	22000	0	22000
33300	0	40800	0	32500	0	43300
51700	0	95000	0	67500	0	46700
103300	1666.67	126700	2500	158300	0	158300
174200	0	193300	0	187500	0	218300
171700	0	199200	0	198300	833.33	236700
138300	833.33	260000	833.33	278300	833.33	226700
192500	0	285000	833.33	292500	1666.67	298300
180000	3333.33	268300	833.33	304200	833.33	249200
180800	833.33	277500	0	243333	833.33	249200
195000	0	264200	0	268300	0	224200
186700	4166.67	214200	5833.33	336700	7500	240800
127500	5000	283300	10000	238300	7500	235000
173300	5833.33	240800	5833.33	260000	8333.33	229200
153300	0	243300	6666.67	204200	10000	220000
150000	9166.67	235000	8333.33	234200	8333.33	237500

Cell and Cyst production of the Ace Lake strain of Pyramimonas gelidicola in different salinity treatments

Cyst no. 40 ppt	Cell no. 50 ppt	Cyst no. 50 ppt	Cell no. 75 ppt	Cyst no. 75 ppt	Cell no. 100 ppt	Cyst no. 100 ppt
0	22000	0	22000	0	22000	0
3333.33	31700	833.33	35800	0	23300	833.33
0	45800	0	55800	0	12500	0
0	98300	0	39200	0	10800	0
0	134200	1666.67	42500	0	16700	0
833.33	162500	1666.67	25800	0	21700	0
0	280000	833.33	60000	7500	8300	0
2500	345000	2500	55000	3333.33	25000	0
0	310000	4166.67	70800	7500	15000	0
833.33	300000	833.33	69200	1666.67	12500	0
0	319200	1666.67	123300	3333.33	11700	0
5833.33	294200	5000	123300	11666.67	10000	0
10833.33	310000	5833.33	155000	18333.33	1700	0
4166.67	278300	833.33	165800	15000	3300	0
9166.67	268300	1666.67	213300	21666.67	6700	0
5833.33	230000	833.33	205800	13333.33	2500	0

Cell and cyst production of the Pyramimonas gelidicola strain from Ace Lake in salinity experiment two.

Age (Days)	Cell no. 50 ppt	Cyst no. 50 ppt	Cell no. 60 ppt	Cyst no. 60 ppt	Cell no. 75 ppt	Cyst no. 75 ppt
0	13500	0	13500	0	13500	0
3	12500	0	6666.6667	0	9166.6667	0
6	7500	0	10833.3333	0	11666.6667	0
8	10000	0	5000	0	3333.3333	0
10	10000	833.333333	6666.6667	0	5000	0
13	10000	0	7500	0	5833.3333	0
15	7500	0	6666.6667	0	5000	0
17	5833.3333	0	2500	0	1666.6667	0
20	5833.3333	0	6666.6667	0	4166.6667	0
22	5000	0	3333.3333	0	833.3333	0
25	6666.6667	0	9166.6667	0	833.3333	833.3333333
28	5000	0	8333.3333	0	833.3333	833.3333333
31	5833.3333	833.3333333	4166.6667	0	1666.6667	0
34	64166.6667	0	5000	833.3333333	833.3333	0
36	92500	0	10833.3333	0	0	0
38	127500	0	10833.3333	0	0	0